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THE UNIVERSITY OF KANSAS
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A Comparative Study of the Throat Musculature in the Plethodontidae of Mexico and Central America

BY

WILMER W. TANNER

ABSTRACT: The paper treats, in detail, of the throat musculature of a number of free-tongued species of Mexican plethodontid salamanders representing the genera, *Bolitoglossa, Magnadigita, Pseudoeurycea, Lineatriton, Chiropterotriton, Parvimolge, Oedipina,* and *Thorius.* The various species in each genus are placed in species-groups, on the basis of similarity of structure, and the generic groups are compared. Some consideration is given to the phylogeny of the genera of the entire family Plethodontidae, based on the characters of the musculature as well as other general characters.

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INTRODUCTION

The Plethodontidae of Mexico and Central America are in general a large and divergent group of free-tongued salamanders. The distribution of this group extends from the Mexican plateau south to the northern Andes and the Amazon basin. Within this vast area there are at present approximately ninety known species, some of which are as yet undescribed. In dealing with these salamanders, the early workers placed them in at least five genera (*Oedipus, Bolitoglossa, Oedipina, Haptoglossa,* and *Thorius*). In the recent monograph of the family by Dunn (1926), all Mexican and Central American plethodontids of the above genera were placed in the genus *Oedipus.* More recently Taylor (1944) restudied these salamanders and not only recognized most of the earlier genera but also described four new genera (*Pseudoeurycea, Chiropterotriton, Parvimolge,* and *Magnadigita*).

I have not seen a representative of the genus *Haptoglossa.* The type of the single species *pressicauda* is lost, and other specimens have not yet been rediscovered. Since I am dealing herein only with the free-tongued species, the genera *Batrachoseps, Haptoglossa* and *Ensatina* are not considered in this study.

The primary purpose of this study is to determine whether or not there are sufficient differences in the throat musculature and the hyobranchial apparatus of the Mexican and Central American genera of the plethodontid salamanders to provide a taxonomic basis for the recognition of the genera, and to show the intrageneric and intraspecific relationships as they are reflected by modifications of the throat myology. My studies have revealed convergences and parallel developments, and I have attempted to correlate these as far as possible with responses to the environmental factors.

The hyobranchial apparatus and the throat musculature of the Mexican and Central American plethodontid salamanders have received relatively little attention from anatomists until recent time. This fact is particularly true with reference to the myology, since only five species have been previously studied, representing approximately six percent of the species known to inhabit this wide area. The earliest account of the throat musculature of a plethodontid was that given in 1875 by Wiedersheim for the single European representative of the family, *Hydromantes genei.* Most of the early myological studies of salamanders were made by Euro-

pean workers on the genus *Salamandra*, a close but primitive relative of the Plethodontidae. These early investigations, while not establishing reliable homologies between groups, did provide the terminology to be used and established a basis for comparison. More recently, "The Anatomy of the Salamanders," by Eric T. B. Francis (1934), has provided a complete anatomical study of the species *Salamandra salamandra*. This work has been of immeasurable value in my studies of plethodontid myology.

The first study dealing with the throat myology of an American plethodontid appears to be that of Emerson (1905) on *Typhlomolge rathbuni*. This species is, however, a perennibranchial salamander, and the study has therefore little application to the present investigation.

An extensive work by Edgeworth (1911) describes and compares the development of the throat muscles from the fishes to the mammals. Edgworth's work is not directly concerned with the plethodontids except as they are similar to *Triton*, but it does deal with various aspects of muscle origin, development and homology, some of which will be considered hereinafter.

In 1920 Miss Louise Smith gave for the first time a detailed account of the hyobranchial musculature of a reasonably specialized plethodontid, in her study entitled "The Hyobranchial Apparatus of *Spelerpes bislineatus*." Equally important to the study of comparative myology was Smith's comparison of the conditions found by Wiedersheim in *Hydromantes* with those of Druner (1904) in *Salamandra maculosa*, and these in turn with the throat myology obtaining in *Eurycea bislineata*. These comparisons and the resulting choice of morphological names represent the first real attempt to arrive at the muscle homologies between the Plethodontidae and the more primitive Salamandridae. Smith also described for the first time the MM. gularis, geniohyoideus medialis and the geniohyoideus lateralis, all of which are peculiar to the family Plethodontidae. The M. subarcualis rectus I (Smith's ceratohyoideus internus) is described in detail, as are other throat muscles of both the larva and adult.

The work by I. W. Wilder (1925) is in reality a confirmation of the work done earlier by Miss Smith and does not add to the known myological facts. The monograph of the family Plethodontidae by Dunn (1926) is almost entirely taxonomic. The short discussion on the myology is very general and is of no particular value to the present study. However, certain distributional and habitat notes are valuable.

By far the most important paper dealing with the comparative myology of the plethodontids is the work, "A Comparative Study of the Hyobranchial Apparatus and Throat Musculature in the Plethodontidae," published in 1935 by Jean Piatt. The study includes an investigation of at least one species and often a comparison of two or more, of all the then accepted genera, save *Leurognathus*. Piatt's purpose was "to furnish an anatomical basis for a slightly different interpretation of the phylogeny within the family Plethodontidae."

According to Piatt the family is divisible into five major groups as follows:

A. *Desmognathus* group, including *Desmognathus* and *Leurognathus*.
B. *Stereochilus* group, including *Stereochilus*, *Typhlotriton* and *Typhlomolge*.
C. *Gyrinophilus* group, including *Gyrinophilus*, *Pseudotriton*, *Eurycea* and *Manculus*.
D. *Plethodon* group, consisting of *Plethodon*, *Hemidactylium*, *Ensatina* and *Aneides*.
E. *Oedipus* group, including *Hydromantes*, *Batrachoseps* and *Oedipus*.

The two genera in group A are very closely related to each other but are obviously not closely related to the genera in any of the other groups. In group E, the allying of *Batrachoseps* with "*Oedipus*" is not proved, and it is a very questionable relationship. As to the relationships of the genera in groups B, C, and D, I have no opinion, since these genera have not been included in this study.

Of the numerous species in the genus *Oedipus* Tschudi, since shown to be preoccupied by *Oedipus* Berthold, (Taylor, 1940:408, Roberts, 1941: 26) and also to be a composite of eight genera, (Taylor 1944:188-232), Piatt examined only five of the eighty known species, and these belong to only three of the eight genera recognized by Taylor (1944). Furthermore, the species of *Oedipus* studied by Piatt were myologically at, or at least near, the two extremes of specialization in that genus. *Pseudoeurycea bellii* and *Magnadigita subpalmata* are two generalized species having few specialized muscles as compared with other species in these two genera, and they are also two of the few species, except for the species of *Thorius*, which do not have a well-developed intermandibularis anterior in all specimens. This fact may have contributed to Piatt's misidentification of the anterior slip of the intermandi-

bularis posterior, for the more anterior muscle. The other three species, all belonging to the genus *Oedipina* (*uniformis, complex,* and *parvipes*), were considered by Piatt (1935:34) to be, on the basis of myology, coenotelic and worthy of reclaiming the name *Oedipina,* synonomized with the genus "*Oedipus*" by Dunn (1926: 432).

Piatt (1939, 1940) published two papers dealing with the "Correct Terminology in Salamander Myology." The first (1939), subtitled "Intrinsic Gill Musculature," is concerned with larvae and perennibranchial urodeles and is not pertinent to this study. His second study (1940), entitled "Transverse Ventral Throat Musculature," is a summary of muscle homologies, which has contributed greatly to a knowledge of the homologies of the transverse muscles. Certain of his conclusions have not been confirmed by my investigations, but these will be considered with the muscles involved.

Eaton (1937) reasoned that the most posterior of the transverse throat muscles should be called the gularis in all urodeles, and that the additional integumentary muscle of the Plethodontidae does not merit a separate name. His evidence was not sufficient to justify his conclusions, and I am convinced, as was Piatt (1940), that there are adequate reasons for retaining the term gularis for a muscle peculiar to the myology of the Plethodontidae. There are certainly five distinct transverse muscles in the adult plethodontids of Mexico and Central America. The gularis, geniohyoideus medialis, geniohyoideus lateralis, and quadrato-pectoralis are peculiar to the lungless salamanders and should not be confused with the analogous muscles of the Ambystomidae and Salamandridae.

Adams (1942) described and compared the hyobranchial apparatus and the throat musculature of *Hydromantes platycephalus* with that of *Hydromantes genei.* The works of Cope (1889) and Hilton (1909, 1946, and 1947) contain several plates showing the hyobranchial skeletons of many genera of plethodontids. Since Hilton's material included six of the currently recognized Mexican genera, his work has been frequently referred to, although there are certain details, particularly in the shape of the ceratohyals, which do not correspond to my observations.

Previous anatomical studies, which have included Mexican and Central American plethodontid salamanders, have been very incomplete and sketchy mainly because of the inadequacy of available material. In spite of the collections made by Dunn, Schmidt, Smith, Stewart, Taylor, and many others, there still remain many

species known only by a few specimens, and there are yet areas in which little collecting has been done. Furthermore, there are few collections containing a series of plethodontid species sufficiently large to provide for an adequate anatomical study. Fortunately, however, there has been accumulated, over a period of years, mainly by the efforts of Dr. E. H. Taylor and Dr. Hobart M. Smith, a large collection of these salamanders in Doctor Taylor's private collections. A few specimens have also been available at the University of Kansas Museum of Natural History. Thus the availability of material as well as the need for further myological studies of these salamanders has been the major impetus for the undertaking of this paper.

MATERIAL AND METHOD

The investigation embodied in this paper is based primarily on the Mexican and Central American Plethodontidae listed herein, although a number of other salamanders have been studied and used as comparative material. Considering the difficulties involved in collecting this type of material, I feel most fortunate in having had such an extensive collection, including at least one specimen of each of the species listed. *Haptoglossa* is the only genus occurring south of the United States which was not available for examination. The throat myology and hyobranchial apparatus of the following eight genera and fifty species has been studied. (Five undescribed species were studied but are not listed):

Pseudoeurycea Taylor
- *P. gadovii* (Dunn)
- *P. unguidentis* (Taylor)
- *P. smithi* (Taylor)
- *P. cephalica cephalica* (Cope)
- *P. bellii* (Gray)
- *P. gigantea* (Taylor)
- *P. cochranae* (Taylor)
- *P. robertsi* (Taylor)
- *P. leprosa* (Cope)
- *P. nigromaculata* (Taylor)
- *P. goebeli* (Schmidt)
- *P. rex* (Dunn)

Chiropterotriton Taylor
- *C. chiroptera* (Cope)
- *C. dimidiata* (Taylor)
- *C. chondrostega* (Taylor)
- *C. arborea* (Taylor)
- *C. terrestris* (Taylor)
- *C. lavae* (Taylor)
- *C. xolocalcae* (Taylor)
- *C. nasalis* (Dunn)
- *C. abscondens* (Taylor)
- *C. multidentata*

Parvimolge Taylor
- *P. townsendi* (Dunn)
- *P. richardi* Taylor

Oedipina Keferstein
- *O. uniformis* Keferstein
- *O. complex* (Dunn)
- *O. serpens* Taylor
- *O. syndactyla* Taylor
- *O. parvipes* (Peters)

Lineatriton Tanner
L. lineola (Cope)

Magnadigita Taylor
M. nigroflavescens (Taylor)
M. macrinii (Lafrentz)
M. engelhardti (Schmidt)
M. rostrata (Schmidt)
M. franklini (Schmidt)
M. subpalmata (Boulenger)
M. dunni (Schmidt)
M. robusta (Cope)

Bolitoglossa Duméril and Bibron
B. mexicana Duméril and Bibron
B. occidentalis Taylor
B. rufescens (Cope)
B. flaviventris (Schmidt)
B. striatula (Noble)
B. platydactyla (Cuvier)

Thorius Cope
T. pennatulus Cope
T. dubitus Taylor
T. troglodytes Taylor
T. pulmonaris Taylor
T. narisovalis Taylor
T. minutissimus Taylor
T. macdougalli Taylor

In addition I have dissected *Ambystoma texanum* (Matthes), *Salamandra salamandra* (Linnaeus), *Plethodon g. glutinosus* (Green), *Batrachoseps a. attenuatus* (Eschscholtz), *Gyrinophilus p. porphyriticus* (Green), *Eurycea l. longicauda* (Green), *Eurycea lucifuga* (Rafinesque), *Desmognathus f. fuscus* (Rafinesque), *Leurognathus m. marmorata* Moore, and *Hydromantes platycephalus* (Camp).

Comparisons have been made with the plates and figures of *Spelerpes bislineatus* prepared by Louise Smith (1920) *Salamandra* by Eric T. B. Francis (1935), *Hydromantes* by Lowell Adams (1942), Cranial muscles of the vertebrates by F. H. Edgeworth (1936), and Plethodontidae by Jean Piatt (1935). Those of Piatt have been particularly useful since there are a large number of genera figured, and one, *Oedipina parvipes,* has direct bearing on this investigation.

I was able to dissect the muscles quite successfully under a binocular microscope without recourse to the use of stains, except for a few muscles. When extremely small muscles could not be delimited or precisely determined, the muscle and the surrounding fascia were removed, stained in a seventy per cent alcohol solution of eosin, and studied under a compound microscope. Such a procedure was invaluable in determining whether or not the fibers of the M. intermandibularis anterior were continuous across the mid-ventral line or whether there was a median raphe present. The presence and extent of the M. rectus cervicis lateralis were also determined by this method. The use of eosin proved very successful in bringing out distinctly the muscle striations. By this method the

muscle fibers were more heavily stained than was the fascia, so that they were readily discerned and could be followed with ease from origin to insertion. Furthermore, since the specimens were preserved in a seventy per cent alcohol solution, the staining could be done in a few minutes. The stained tissues were stored in small vials of dilute eosin solution from which they could be removed and studied as desired.

For each specimen studied in detail, the characteristics of fifteen throat muscles and of the hyobranchial cartilages were recorded. Each muscle was investigated to determine as accurately as possible the origin, insertion, size, shape, and relationships to other muscles. The position and extent of the muscles are all stated in terms of their relation to a common structure; for example, the mental symphysis or the posterior tip of the mandible. In no instance was an attempt made to determine the relative lengths of muscles between species, unless the difference in relative length was apparent. Though a study of the relative lengths of muscles may be desirable, its full usefulness as a character is not attainable unless sufficient individuals of each species are measured to determine the individual variation within a species. In most species examined I have seen only one specimen, and it has, therefore, not been possible to determine accurately the degree of variation among the individuals of a given species. I have utilized as characters only those muscle relations which seemed least variable. The relative lengths of the posterior segment of the M. rectus cervicis to the two anterior segments of the same muscle proved significant and was used throughout the study.

MUSCLE TERMINOLOGY

The muscles examined are, except for the gularis, quadratopectoralis, geniohyoideus lateralis, and the rectus cervicis lateralis, homologous to the muscles of the more primitive *Salamandra.* It is for this reason that the work of Francis (1934) has been so useful in this study. The names of the muscles studied and the authority for each has been determined by usage and by the appropriateness of the term. I have followed for the most part the published studies of Francis, Drüner, Edgeworth, Smith, and Piatt in arriving at the terms used.

In order to prevent unnecessary repetition of characters common to most of the genera and to review briefly muscle homologies and authorities, the following list of throat muscles is presented in advance of the general description given for each genus studied.

THE TRANSVERSE THROAT MUSCLES

M. intermandibularis anterior (Drüner 1901).

According to Piatt (1940:10) the intermandibularis anterior disappears completely at metamorphosis in the families Hynobiidae, Ambystomidae, Salamandridae and Plethodontidae, leaving the intermandibularis posterior as the most anterior of the transverse throat muscles. Although this may be true of the first three families, it is certainly not the condition in all genera of the family Plethodontidae. I have observed the anterior muscle in adults of at least one species of the following genera: *Pseudoeurycea, Chiropterotriton, Parvimolge, Magnadigita, Bolitoglossa, Oedipina, Batrachoseps* and *Lineatriton*. It was not present in the species of *Plethodon, Gyrinophilus, Eurycea* and *Hydromantes* which I examined. When present, this muscle lies along the anterior edge of the anterior slip of the intermandibularis posterior and is usually widest at the mid-ventral line. The muscle always arises in fascia a short distance medial to the mandible and is usually without a median raphe.

The fact that this muscle is absent in nearly all adult plethodontids living in the United States and is often absent in the two species (*Magnadigita subpalmata* and *Pseudoeurycea bellii*) studied by Piatt (1935:216) may explain in part the misunderstanding concerning this muscle in the family Plethodontidae.

In the family Desmognathidae a small straplike muscle extends from the mid-ventral line, immediately caudal to the symphysis, anterolaterad across the ventral surface of the mandible, and attaches to the anterolateral surface of the mandible. The median raphe is distinct, and there is a short distance separating this muscle from the anterior slip of the intermandibularis posterior. Whether the muscle described represents the intermandibularis anterior or a modification of the anterior part of the anterior slip of the intermandibularis posterior is as yet uncertain. Its position is, however, very suggestive of the intermandibularis anterior. Equally important is the fact that this muscle arises from the anterolateral surface of the mandible and extends across the ventral surface of the mandible. Such a condition is unique among the lungless salamanders and should be added to the family characteristics of Desmognathidae. Soler (1949) figures the superficial transverse throat muscle of *Desmognathus o. ochrophaeus* and represents this anterior muscle as I have found it in *Desmognathus f. fuscus* and *Leurognathus m. marmorata*.

M. intermandibularis posterior (Drüner 1901).

This muscle is always divided into a small anterior and a much larger posterior slip, both of which are fan-shaped, and together they occupy most of the area between the mandibular rami. Both arise from the dorsomedial surface of the mandible and insert in the ventral aponeurosis.

M. gularis (Smith 1920).

The gularis is a muscle peculiar to the plethodontids and is, according to Piatt (1935:223, 1940:10), a derivitive of the larval interhyoideus posterior, arising at the time of metamorphosis. The muscle takes its origin in fascia, with approximately the anterior half of the muscle arising in a thin sheet of fascia covering the greater part of the M. depressor mandibulae anterior. The major part of this thin sheet of fascia is in turn attached to a heavier fascia lying between the edges of the MM. depressor mandibulae and capiti mandibularis. The anterior fibers are usually not far posterior or anterior to the posterior tip of the mandible and their insertion is commonly at or near the mid-ventral line.

M. depressor mandibulae (Humphrey 1872).

In all genera of Mexican and Central American plethodontids, the depressor mandibulae is divided into two distinct muscles. Previous workers have referred to these divisions as slips, but this situation, in view of the entirely separated condition of the muscle, plus the fact that both muscles have very different origins and are separable from the origin to the insertion, is not representative of the true condition. I am therefore designating them as distinct muscles according to their position as the anterior and posterior muscle.

M. depressor mandibulae anterior (new name).

The anterior muscle arises from the squamosal and the lateral edge of the otic capsule. The part of the muscle arising from the otic capsule is usually deep to the M. cucularis major. The insertion is on the dorsal surface of the posterior tip of the mandible.

M. depressor mandibulae posterior (new name).

The posterior muscle arises from the fascia cephalodorsalis between the anterior muscle and the gular fold. It is entirely superior to the M. cucularis major. The insertion is on the ventral surface of the posterior tip of the mandible.

M. quadrato-pectoralis (Drüner 1901).

This muscle is large and is readily distinguished from the interhyoideus in all Mexican and Central American plethodontids. According to Piatt (1935:223) the quadrato-pectoralis "has not quite

disappeared from even the specialized end genera, such as *Oedipus* and *Manculus,* but it has been so reduced functionally that its identity as a distinct element is almost negligible." Such a condition is not found in the Mexican and Central American species. I have found this muscle to be well developed, and its size indicates that it is a functional muscle. The variation in the point of origin has undoubtedly led to a masking of this muscle in many species, and I suspect, as in the case of *Hydromantes* and in other more northern genera, that the origin has shifted entirely to the ceratohyal and is therefore confused with that of the interhyoideus. If we accept Piatt's (1935 and 1940) reasoning that the interhyoideus posterior at metamorphosis is divided into two muscles, the gularis and the quadrato-pectoralis, and that the interhyoideus is retained in all plethodontids, then we have the conditions obtaining in the eight genera of Mexican and Central American Plethodontidae herein considered. This is in contrast to the more northern genera in which this muscle is lost (according to Piatt) in some, fused and nearly inseparable in others (*Hydromantes*) and having an entirely different arrangement in still others (*Aneides*).

In the Mexican and Central American genera, at least part of the origin of this muscle is always on the quadrate or the squamosal, but more often it arises from both bones. There are usually a few fibers arising from the tendinous sheath surrounding the ceratohyal at the point of its attachment onto the skull, but these fibers are always distinctly separated from the anterior fibers of the more posterior interhyoideus. In the more generalized species the origin is primarily, if not completely, on the posterior edge of the quadrate; this may justify, at least, the "quadrato" part of the name. The major part of the insertion is always in the ventral aponeurosis between the intermandibularis and the gularis.

M. interhyoideus (Drüner 1901).

The interhyoideus arises on the ceratohyal between the lateral curvature of the ceratohyal posterior to the caudal tip of the mandible and the attachment of the ceratohyal to the skull. The insertion is usually deep to the posterior slip of the intermandibularis posterior and is often broad and fan-shaped. This muscle in plethodontids has been found to be smaller than the quadrato-pectoralis and is unique in having a peculiar decussation of the fibers at or near its belly. Those fibers arising on the anterior edge of the muscle extend in a nearly transverse direction, whereas those on the posterior border extend in a nearly longitudinal direction and

cross dorsally over the anterior fibers to insert as the anterior part of the muscle, thus reversing completely the order of the muscle fibers at the insertion. This one hundred and eighty degree rotation is present also in *Hydromantes* and may be used to separate the interhyoideus from the closely associated anterior fibers representing what remains of the quadrato-pectoralis in that genus.

THE LONGITUDINAL AND DEEP MUSCLES

M. geniohyoideus medialis (Smith 1920).

The medialis arises from the posterior or ventral surface of the mandible lateral to the symphysis. The width of the origin is extremely variable. The lateral part of the insertion is on the ventral surface of the subarcualis rectus I, whereas the medial part is inserted along the anterior edge of the inscriptio tendinis. The lateral part of the insertion is usually posterior to the caudal tip of the mandible and is commonly lateral to the mid-ventral line.

The inscriptio tendinis is a connective tissue mass which lies in a more or less transverse position approximately ventral to the second ceratobranchial. It represents the ligamentous vestiges of the second basibrancial, often called the os thyroideum, and is a bony structure in some plethodontids. The inscriptio tendinis is an important structure and appears to serve a double function. It is first of all an area for insertion of the geniohyoideus medialis, the medial part of the subarcualis rectus I, the medial part of the rectus cervicis, and the small ventral slip of the abdominohyoideus. Secondly, it appears to serve as a transverse support for the throat region, since it is securely attached to the medial side of each subarcualis rectus I and also at the mid-ventral line. The condition described for *Hydromantes* by Adams (1924:189) is similar to that found in the Mexican and Central American genera.

M. geniohyoideus lateralis (Smith 1920).

The lateralis arises from the posterior, ventral and medial surfaces of the mandible and it is usually laterad and dorsad to the medialis. The extent of the attachment on the mandible is extremely variable. The insertion is on the lateral edge and on the dorsal surface of the ceratohyal. A few of the medial fibers are commonly extended posteriorly to the ceratohyal and are inserted on the floor of the pharynx.

The names of the geniohyoideus muscles here employed are those used also by Piatt (1940). Piatt has described the ontogenetic development of the geniohyoideus muscles in Plethodontidae in some detail, and I see no reason for questioning his reasoning and conclusions.

M. rectus cervicis superficialis (Edgeworth 1928).

The superficialis is a very thin sheet of muscle fibers arising entirely from the anterolateral edge of the sternum and becoming fused with the deeper profundus muscle at the first myocomma anterior to the sternum. This muscle is present in all genera of Mexican and Central American plethodontids studied, but is, at times, not easily separated from the profundus.

M. rectus cervicis profundus (Edgeworth 1928).

The major portion of this muscle is a direct anterior continuation of the rectus abdominis. It is inserted on the ventral surface of the subarcualis rectus I and along the posterior edge of the inscriptio tendinis.

M. rectus cervicis lateralis (new name).

In the course of this investigation it was noted that the M. omohyoideus is not present in the species of Plethodontidae of Mexico and Central America which I have examined. In *Salamandra salamandra* and *Ambystoma texanum* the omohyoideus arises from the medial surface of the ventral end of the scapula and is inserted along the lateral edge of the superficial portion of the M. rectus cervicis (fig. 1). The anterior end of the insertion is at the level of the os thyroideum, whereas the posterior end is at the first myocomma of the rectus cervicis, anterior to the sternal cartilage. In these species the insertion is approximately twice the width of the origin.

A small slip of muscle arising on the edge of the sternum immediately laterad to the M. rectus cervicis superficialis, and extending anterolaterad to the lateral surface of the M. abdominohyoideus where it is inserted in fascia approximately at the level of the thyroid gland, was noted in most genera of Plethodontidae and in the family Desmognathidae. This muscle is not recognizable either in *Salamandra* or *Ambystoma,* but in *Desmognathus f. fuscus* it appears as a well-defined muscle extending from its origin on the sternum along the lateral edge of the rectus cervicis to the ventral surface of the medial end of the first ceratobranchial, where it is inserted (fig. 2). Particularly noteworthy is the presence of a myocomma anterior to the sternum, which corresponds to the first myocomma of the rectus cervicis. Equally significant is the insertion of the now reduced omohyoideus at the first myocomma of the lateral muscle. The muscles just described for *Desmognathus fuscus* are also present in *Plethodon g. glutinosus, Gyrinophilus p. porphyriticus,* and *Batrachoseps a. attenuatus* but are reduced in size, especially in *Batrachoseps.* In *Eurycea l. longicauda* the omo-

hyoideus is further reduced, but its relationships remain unchanged. The lateral slip has also become reduced in size and is now inserted in the fascia on the lateral surface of the M. abdominohyoideus (fig. 3). In the case of the insertion the lateral slip has now reached a developmental stage comparable to the condition obtaining in the plethodontid genera of Mexico and Central America, and it is only a case of losing the small omohyoideus before reaching the condition existing in the genus *Pseudoeurycea* (fig. 4).

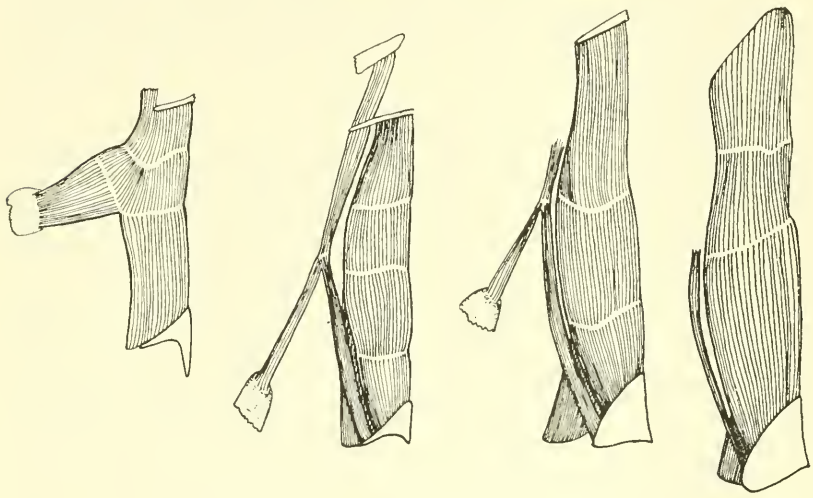

Fig. 1 Fig. 2 Fig. 3 Fig. 4

FIG. 1. The muscle omohyoideus (left), and m. rectus cervicis in *Ambystoma texanum*. The m. rectus cervicis lateralis is absent.

FIG. 2. Characteristics of the m. rectus cervicis lateralis in *Desmognathus f. fuscus* showing the reduction of the omohyoideus.

FIG. 3. Characteristics of the m. rectus cervicis lateralis in *Eurycea l. longicauda* showing the reduction of the omohyoideus.

FIG. 4. Characteristics of the m. rectus cervicis lateralis in the genus *Pseudoeurycea* and the complete loss of the omohyoideus.

In summary, two points are evident: First, the omohyoideus is slowly reduced from *Desmognathus* through the more generalized plethodontids to *Eurycea* and finally is lost in the adults of the genera (*Pseudoeurycea* for example) considered in this study. Second, the lateral slip as seen in the Plethodontidae is distinct from the main body of the M. rectus cervicis superficialis, but since it is undoubtedly a specialized muscle derived from the rectus cervicis superficialis, it may be appropriately named the *rectus cervicis lateralis.*

M. abdominohyoideus (Smith 1920) (pl. LXVIII, fig. A).

The most striking and certainly the longest muscle in these salamanders is the abdominohyoideus. It arises on the medial and posterior margins of the ischiopubic plate and extends anteriorly along the lateral edge of the rectus abdominis and the posterior part of the rectus cervicis profundus. At approximately the level of the posterior tip of the thyroid gland, or slightly posterior in a few species, the abdominohyoideus curves medially deep to the rectus cervicis and often becomes convoluted or folded before passing ventrad to the second ceratobranchial and dorsad to the first ceratobranchial as the muscle extends anteriorly parallel to the elongate first basibranchial. The abdominohyoideus is inserted in a short tendon, which is in turn attached to the ventral surface of the tongue anterodorsal to the tip of the basibranchial. A ventral slip becomes separated from the main body of the muscle at, or a short distance anterior to, the level of the sternal cartilage and is inserted in the inscriptio tendinis.

The abdominohyoideus muscle is so uniform throughout all the genera studied that it is not included in the generic descriptions. The only important variations noted in this muscle were those associated with the level at which the ventral slip diverges from the main body of the muscle.

M. subarcualis rectus I (Edgeworth 1920).

This muscle has become specialized throughout the family and has reached a high degree of development in all Mexican and Central American plethodontids. The muscle arises on the ventral surface of the ceratohyal, beginning along the medial margin and extending across to the lateral edge approximately at the level of the anterior edge of the suprapeduncularis. It continues posteriorly along the lateral edge of the ceratohyal to a point near the level of the posterior tip of the mandible. The insertion is medially along the inscriptio tendinis and is laterally on the distal ends of the ceratobranchials and the tendinous sheath enclosing the epibranchial.

The size, particularly the length, is exceedingly variable among the genera and has been used as an important diagnostic character.

M. suprapeduncularis (Smith 1920).

The origin of the suprapeduncularis is on the dorsomedial surface of the ceratohyal a short distance posterior to its proximal end, and it is extended posteriorly for a short distance, usually for approximately the same length as the longest fibers of the muscle. The length and width as well as the shape of the muscle are vari-

able, and there is always a characteristic "U" or "V" shaped indentation along the anterior margin of the muscle. The suprapeduncularis is distinct and is not in any way fused with the pharyngeal fibers of the throat area. In fact, there are few pharyngeal fibers in most genera that could in any way be confused with the posterior fibers of the suprapeduncularis muscle.

M. hyoglossus (Fischer 1843).

This muscle usually arises on the anterior end of the basibranchial between the cornua, and it inserts in the anterior semicircle of the tongue. Though I have not been able to observe the action of the tongues of these salamanders, the ventral position of the hyoglossus muscle suggests its obvious function; as the tongue is forced from the mouth the hyoglossus contracts to pull the dorsal horizontal surface to a vertical position and thus provides an efficient feeding apparatus. This is important because this surface of the tongue is richly supplied with a sticky mucous which is most essential in holding food items until they are pulled into the mouth.

THE HYOBRANCHIAL SKELETON

The cartilaginous hyobranchial skeleton is composed of the elongate and rounded first basibranchial; two ceratohyals, which are flattened in the middle, attenuated and hooked on the distal end, and variously flattened or attenuated on the proximal end; a small round first ceratobranchial with the proximal end slightly flattened; and a larger round second ceratobranchial and a greatly elongated rod-shaped epibranchial, which articulates proximally with the distal ends of the ceratobranchials and usually extends to or posterior to the anterior edge of the front leg when the leg is at right angles to the body. The second basibranchial is missing in all genera and is represented by a vestige of connective tissue called the inscriptio tendinis. The lingual cartilage is also missing in all Mexican and Central American genera of Plethodontidae.

Certain statements made by Piatt (1935:228) are not entirely correct when representatives of all the Mexican and Central American plethodontids are carefully examined. First, the cornua on the anterior tip of the basibranchial are not "rather short" but are extremely short in *Thorius*, and are long and curved in some *Bolitoglossa*. Second, the ceratohyals are not "extremely slender" in most forms. The ceratohyals of typical *Oedipina* are the most slender of all examined, and since three of the five species seen by Piatt were of this genus, this may have been the influencing factor.

I have found the proximal third of the ceratohyals to vary suffi-

ciently to allow use of the variation as reliable taxonomic characters. The ceratohyals are long and attenuated in the more specialized genera of *Thorius* and *Oedipina,* but with this difference: in *Thorius* the proximal ends of the ceratohyals are round and rodlike, whereas in *Oedipina* they are slightly flattened and are noticeably wider than thick. In *Bolitoglossa* and *Magnadigita* the ceratohyals are shorter and terminate in a bluntly rounded end with little or no flattening proximally. In the other genera (*Pseudoeurycea, Chiropterotriton, Lineatriton* and *Parvimolge*) the proximal end is lengthened and flattened in various ways depending on the genus. In *Pseudoeurycea* and *Parvimolge* the ceratohyal ends proximally in a nearly symmetrical lobe, but is not exactly spatulate; therefore, I have referred to this proximal lobe as a "spade" in these genera. In *Chiropterotriton* the anterior lobe is not symmetrical, and because it is more flattened medially than laterally, I have referred to it as a "bladelike" structure.

The middle part of the ceratohyal in all genera of Mexican and Central American plethodontids, save *Oedipina,* is broad, with a medial lobe extending nearly to the mid-line in some species.

The distal third of the ceratohyal is always slender, attenuated, and usually it has a sharp curve a short distance caudad to the posterior tip of the mandible. The distal end is always attached to the skull either directly or by a ligamentous sheath and is with few exceptions attached to the squamosal, although in some of the more primitive species it is difficult to determine whether it is attached to the quadrate or the squamosal, or whether it actually articulates with both. It is certainly not attached to the quadrate in all species as suggested by Cope (1889:120).

ACKNOWLEDGMENTS

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DESCRIPTION OF THE THROAT MYOLOGY AND THE HYOBRANCHIAL CARTILAGES

The Genus *Pseudoeurycea* Taylor

Pseudoeurycea Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, no. 12, 1944, p. 209 (type *Spelerpes leprosus* Cope).

The genus *Pseudoeurycea* includes a large assemblage of rather diverse but generalized terrestrial species. As a whole they are characterized by having the toes unwebbed beyond the metatarsals or metacarpals. In certain forms the webbing may extend on to the first phalanges of the outer fingers and toes but the middle digits are usually free. The distal phalanges are provided with rounded or ovate subterminal pads, while the palms and soles are smooth and unspecialized. There is a large sublingual fold present beneath the outer and anterior margins of the tongue. The species are moderate to large in size, in fact the largest plethodontid salamanders known, *P. bellii* and *P. gigantea*, belong to this genus.

The following muscle descriptions represent the general conditions obtaining in the genus. Any noteworthy departures from, or specializations of, the usual arrangement will be indicated.

TRANSVERSE THROAT MUSCLES

M. intermandibularis anterior (pl. LXVIII, fig. D; pl. LXIX, figs. B, C, & I).

The origin of this muscle is in fascia along the anterior margin of the anterior slip of the intermandibularis posterior. In all species the fascia extending laterad from the origin to the mandible becomes fused with the fascia on the anterior and dorsal surfaces of the anterior slip. There is no indication of a median raphe, except in *goebeli*, and *rex*, in which the posterior part of the muscle is divided at the mid-ventral line. It is doubtful whether this muscle is present in *cephalica cephalica* and *robertsi*. It was not present in the specimens that I examined. In *bellii* the males have this muscle well developed, whereas in the female it is present in only approximately half of the specimens examined and is in a much reduced condition when compared with the muscle in the males. This condition may exist in both *cephalica* and *robertsi* in which I have seen only female specimens. This muscle reaches its greatest size in *leprosa*, and is, with the lone exception of *robertsi*, well developed in all the species closely related to *leprosa* (*goebeli, rex, nigromaculata* and *cochranae*). There is less specialization of this muscle in *Pseudoeurycea* than in any of the genera studied save *Thorius* where it is totally absent.

M. intermandibularis posterior (pl. LXVIII, fig. D; pl. LXIX, figs. B, C, & I).

The anterior slip originates on the dorsomedial surface of the mandible approximately one third of the length of the mandible caudad to the symphysis. The insertion is in the ventral aponeurosis and anteriorly at the mid-ventral line. The proportion of fibers reaching the mid-line varies among the species. Approximately one fourth of the fibers reach the mid-line in *bellii* and *gadovii,* while in *rex* and *goebeli* only the most anterior fibers reach the mid-line.

The posterior slip originates on the dorsomedial surface of the mandible, beginning at a point 1 or 2 mm. anterior to its posterior tip and extending craniad for approximately one third the length of the mandible. The insertion is in the ventral aponeurosis, and with no fibers reaching the mid-ventral line, although they approach more closely this line in *Pseudoeurycea* than in any of the genera studied.

M. gularis (pl. LXVII, fig. D; pl. LXIX, figs. B, C, & I).

The origin of the anterior part arises in a thin sheet of fascia whereas the posterior part originates in the fascia cephalodorsalis. The fascia cephalodorsalis is a term used by Drüner to designate the fascia extending caudad from near the otic capsule to the gular fold, beneath the horizontal postocular skin groove and which lies immediately ventrolaterad to the dorsalis trunci muscles. Several muscles have part or all of their origin in this fascia. The thin fascia extending from the anterior part of the gularis is attached to the lateral edge of the mandible; to the quadrate; to the squamosal between the MM. depressor mandibulae and the capitis mandibularis, and to the lateral edge of the otic capsule. The thin fascia disappears shortly caudad to the skull. The insertion is on the skin of the gular fold and along the linea alba. The proportion of the muscle inserted at the linea alba is variable. In *bellii* and *gigantea* there is approximately one fourth of the total insertion at the linea alba while in *goebeli* there is less than one fifth of the muscle inserted here.

In *Pseudoeurycea* the gularis is large, both the origin and the insertion being extensive, and there is a large proportion of the muscle inserted at the linea alba.

M. depressor mandibulae anterior.

The anterior muscle originates chiefly on the dorsolateral surface of the squamosal and the lateral edge of the otic capsule. The fibers arising from the latter are usually deep to the cucularis major. In most species a few fibers arise from the posterior edge

of the quadrate. The insertion is on the dorsal part of the posterior tip of the mandible.

M. depressor mandibulae posterior.

The posterior muscle originates in the fascia cephalodorsalis deep to the gularis but superior to the cucularis major. The insertion is on the posterior tip of the mandible ventral to the insertion of the anterior muscle.

The depressor mandibulae muscles are uniformly developed throughout the genus *Pseudoeurycea* with the exception of *robertsi*. In *robertsi* the division of the two muscles is not clearly marked and the dorsal part of the anterior muscle does not lie deep to the cucularis major.

M. quadrato-pectoralis (pl. LXVIII, fig. D; pl. LXIX, figs. B, C, & I).

The origin of the quadrato-pectoralis is variable. In most species the larger portion of this muscle is on the posterior surface of the dorsal end of the quadrate. In many other species a few fibers arise from the posteroventral edge of the squamosal and from the fascia surrounding the tip of the ceratohyal. In *gigantea*, *bellii* and *smithi* the origin is entirely on the quadrate, while in *cochranae* and *rex* it is mainly on the squamosal. The insertion is in the ventral aponeurosis between the intermandibularis posterior and the gularis. The anterior fibers are inserted deep to the intermandibularis posterior except in *cochranae*.

The attachment of this muscle on the quadrate is another of the several primitive conditions existing in *Pseudoeurycea*. There appears to be a well-established phylogenetic relationship leading from the most primitive or generalized species, *bellii* and *gigantea*, through to the more specialized *cochranae* and *rex* of group III.

M. interhyoideus (pl. LXVIII, fig. D; pl. LXIX, figs. B, C, & I).

The origin of the interhyoideus is on the anteroventral surface of the anteriorly projecting distal end of the ceratohyal. The origin extends from a point near the attachment of the ceratohyal to the skull, caudoventrally to the lateral curve or hook of the ceratohyal posterior to the skull. The anterior fibers arise near the posterior fibers of the quadratopectoralis but there is a clear distinction between the origins of the two muscles. The insertion is in the ventral aponeurosis deep to the posterior slip of the intermandibularis posterior. The insertion is broad, extending almost to the anterior edge of the posterior slip.

THE LONGITUDINAL AND DEEP MUSCLES

M. geniohyoideus medialis (pl. LXXI, figs. A, C, & E; pl. LXXIII, fig. H).

The origin of the medialis is on the posterior surface of the mandible lateral to the symphysis and always anterior to the origin of the anterior slip of the intermandibularis posterior. The insertion extends from the lateral edge of the subarcualis rectus 1 medially across its ventral surface and along the anterior edge of the inscriptio tendinis. The insertion extends medially to the midventral line in *bellii, gigantea, leprosa* and *cephalica* and is partly or entirely posterior to a line between the posterior tips of the mandibles in all except *rex*. In this species the lateral part of the muscle extends only to the posterior tip while in *nigromaculata* the entire insertion is considerably anterior to such a line.

M. geniohyoideus lateralis (pl. LXXI, figs. A, C, & E; pl. LXXIII, fig. H).

The origin of the lateralis is on the posterior edge of the mandible dorsal and lateral to the medialis and anterior to the anterior slip of the intermandibularis posterior in all species. The medial half, or more, of this muscle arises dorsal to the medialis in all species except *nigromaculata* in which only a small fraction is dorsal. The insertion is on the lateral edge of the ceratohyal, beginning posterior to the caudal end of the mandible and extending anteriorly to near the middle of the cartilage. In *nigromaculata* the insertion is entirely anterior to the posterior tip of the jaw.

M. rectus cervicis superficialis (pl. LXXI, figs. A, C, & E).

The origin of this muscle is on the anterolateral edge of the sternum. In *bellii, gigantea, gadovii, unguidentis* and *cephalica* this muscle entends anteriorly and anterolateraly to cover the profundus muscle at the first myocomma anterior to the sternum. In the species of group III, the superficialis does not reach to the lateral edge of the profundus at the first myocomma, and there is a noticeable reduction in the size of the sternum and the relative width of the superficialis at its origin. In *smithi* the two muscles are not clearly separable into a superficialis and a profundus. In all species studied the superficialis is fused with the profundus anterior to the first myocomma and extends with it to a common insertion.

M. rectus cervicis profundus (pl. LXXI, figs. A, C, & E).

In *Pseudoeurycea* the profundus is almost entirely a continuation

of the rectus abdominis muscles, with only a few fibers arising from the lateral edge of the sternum. In *gigantea* no fibers arise from the sternum or any of the lateral fascia attached to it. The insertion is on the medial part of the subarcualis rectus 1 and extends medially along the posterior edge of the inscriptio tendinis to the mid-ventral line.

The rectus cervicis is divided into three unequal segments by two myocommata. The posterior segment is approximately as long as the combined lengths of the two anterior segments, the middle segment being the shortest. From the medial part of the anterior myocomma deep to the main mass of the rectus cervicis is a small slip extending deep to the second ceratobranchial and inserted on the floor of the mouth a short distance posterior to the ceratohyals and suprapeduncularis. In *bellii* this slip inserts on the posterior edge of the ceratohyals immediately caudal and lateral to the posterior fibers of the suprapeduncularis, while in *gigantea* only a few lateral fibers reach the ceratohyals, the medial fibers being inserted on the floor of the mouth. In *bellii* and *gigantea* the muscle is also proportionally larger and wider than it is in other species. This size difference is particularly noticeable when compared with the species of group III.

M. rectus cervicis lateralis (pl. LXXI, figs. C, & E).

The origin of the lateralis is on the edge of the sternum immediately lateral to the rectus cervicis superficialis. From the origin it extends diagonally across the rectus cervicis profundus and anteriorly along the lateral surface of the abdominohyoideus approximately to the level of the thyroid gland where it is inserted in fascia. It has been difficult to determine accurately the insertion, chiefly because of the small size of the muscle and also owing to a peculiar branching of the fibers at or just before the insertion.

M. subarcualis rectus 1 (pl. LXXI, fig. A; pl. LXXII, fig. F; pl. LXXIII, figs. B, E & H; pl. LXXIV, fig. C).

The origin of this muscle is on the ventral surface of the ceratohyal, beginning at the base of the anterior ovate "spade" of the ceratohyal and extending caudad along the lateral edge of the ceratohyal to a point beyond the posterior tip of the mandible. A smaller part extends caudad along the medial edge of the ceratohyal approximately to the posterior edge of the suprapeduncularis. In *nigromaculata* and *rex* the posterior fibers are attached to the man-

dible a short distance anterior to its posterior tip. The insertion extends along the anterior edge of the inscriptio tendinis to the distal ends of the ceratobranchials and in the tendinous sheath of the epibranchial. The insertion extends medially to, or nearly to, the mid-ventral line. The muscle is noticeably elongate and extends well beyond the posterior level of the insertion of the arm in all species.

M. suprapeduncularis (pl. LXXII, fig. F; pl. LXXIII, figs. B, E & H; pl. LXXIV, fig. C).

This muscle arises on the dorsomedial surface of each ceratohyal and extends transversely dorsal to the tongue stalk. In *Pseudoeurycea* the suprapeduncularis is well developed and is easily distinguished from any other tissues in the pharyngeal region of the mouth. The anterior fibers are longest and are curved caudomedially to produce a U-shaped anterior border. The fibers become progressively shorter and more transverse caudad. The muscle extends from the base of the expanded anterior "spade" of the ceratohyals posteriorly for a distance approximately equal to the length of the fibers or, as in *nigromaculata*, until the medial lobes of the ceratohyals are almost approximating each other immediately posterior to the muscle. In *nigromaculata* and *rex* the ceratohyals are rather close together and the suprapeduncularis appears as a wide, greatly shortened muscle.

M. hyoglossus.

The origin of the hyoglossus is on the anterior tip of the basibranchial between the cornua. The insertion is in the tongue tissue anterodorsal to the origin. This is a well-formed, narrow muscle, several fibers thick at the origin and fanning out into a thin broad muscle at the insertion.

In *Pseudoeurycea* the ceratohyals are elongate, attenuated posteriorly and, with the exception of *nigromaculata*, curved at less than a right angle posterior to the caudal end of the mandible. The anterior end is expanded into a broad flattended spade, the medial edges of which extend nearly to the mid-ventral line. In *nigromaculata* the entire anterior half of each ceratohyal is expanded into a more flattened and broader spadelike structure than is to be seen in other species of the genus. Furthermore, in *nigromaculata* the ceratohyals extend to the posterior edge of the mandible near the symphysis, a condition most unusual in this genus.

SUMMARY

On the basis of the throat myology and the structure of the ceratohyals it is possible to arrange the species of *Pseudoeurycea* into the following three groups:

Group I	
bellii	*smithi*
gigantea	
Group II	
gadovii	*cephalica*
unguidentis	
Group III	
leprosa	*goebeli*
robertsi	*rex*
cochranae	*nigromaculata*

The species of group I are apparently the most generalized of the genus. The origin of the quadrato-pectoralis on the quadrate, the broad insertion of the anterior slip of the intermandibularis posterior, the insertion of the gularis at the mid-ventral line and the relatively large rectus cervicis lateralis are all primitive characters. A consideration of each character separately may make it possible to point out more clearly the reasons for such conclusions.

In the more generalized genera of the family Plethodontidae, *Plethodon* for example, the quadrato-pectoralis arises from the posterior edge of the dorsal tip of the quadrate and the ligamentous tissue surrounding the tip of the ceratohyal. Furthermore, a line of distinction is not apparent between the quadrato-pectoralis and the interhyoideus, especially at their origin along the distal end of the ceratohyal and the quadrate. The two muscles are separate in both *bellii* and *gigantea*, but the quadrato-pectoralis has continued to maintain a primitive origin.

I have come to regard broad insertions at the mid-ventral line as primitive, mainly because of the broad insertions found in Salamandridae, a family known to be more primitive than Plethodontidae and considered by many to be the ancestral stock from which the Plethodontidae arose. In the larvae of the Salamandridae, and in the Ambystomidae, all of the superficial transverse throat muscles are inserted at the median raphe. If such a condition existed in the ancestral stock, then the extent of departure from such a pattern would indicate the degree of primitiveness in more specialized species. There is a possibility of a secondary speciali-

zation, but I can see no reason for considering such a possibility when other factors point to an obviously primitive condition.

The rectus cervicis lateralis reaches a greater degree of development in *Pseudoeurycea* than in any of the genera considered herein. It is a large muscle and is easily traced from the origin to the insertion, especially in the larger species. In *smithi* the rectus cervicis lateralis is small, approximately one third the size of that obtaining in a specimen of *bellii* of the same length. Except for this one character, *smithi* is much the same as *bellii*, to which it appears to be most closely related.

The species of group II are also rather primitive and are, on the basis of myology, more closely related to group I than to group III. In these species the origin of the quadrato-pectoralis is principally on the quadrate, but with a few posterior fibers arising from the squamosal. The rectus cervicis lateralis is small, but the insertion of the transverse muscles along the mid-ventral line is broad.

Group III represents the most specialized species in the genus *Pseudoeurycea*. Except for *robertsi*, the intermandibularis anterior is present and larger than in the species of group II. In *gigantea* and in the males of *bellii* this muscle is approximately the same relative size as it is in the species of group III. In *leprosa* and *nigromaculata* the anterior muscle has become triangular in shape and is strikingly similar to that found in *Chiropterotriton multidentata* and *C. terrestris*. It appears to be a result of an adaptation to similar environmental situations.

In group III the origin of the quadrato-pectoralis is almost equally divided between the quadrate and the squamosal. In *leprosa* and *goebeli* a larger part arises from the quadrate, whereas in *cochranae* and *rex* almost the entire muscle originates on the squamosal. The insertions at the median raphè are narrower, and the rectus cervicis lateralis is very small (largest in *leprosa*).

A further difference between the groups is the length of the posterior segment of the rectus cervicis in proportion to the rest of the muscle. In group III the posterior segment is, save for *nigromaculata*, always less than half the length of the entire muscle. In the other groups the posterior segment is approximately half, or as in *smithi* noticeably more than half, the length of the entire muscle.

The two most divergent species in group III are *nigromaculata* and *robertsi*. The species *leprosa, goebeli*, and *cochranae* are the most closely related in the group. In *rex* and *goebeli* a division of the posterior half of the intermandibularis anterior at the median

raphe has led me to suspect that the absence of this muscle in *robertsi* is more apparent than real, and it is actually completely divided and fused with the anterior slip of the intermandibularis posterior. It is possible that an examination of a series of individuals of this species would reveal some specimens with the muscle developed. At present I can offer no explanation for the unusual divergence existing in *nigromaculata*.

The GENUS *Chiropterotriton* Taylor

Chiropterotriton Taylor, Univ. Kansas Sci. Bull., vol. 30, no. 12, 1944, p. 213 (type *Oedipus multidentatus* Taylor).

This genus includes, at present, twelve species of small terrestrial and arboreal salamanders. The digits of hand and foot are widely spread, usually truncate, and bear small subdigital pads under the terminal phalanges. The proximal phalanges and the entire first finger and toe are included in the smooth pad of the palm and sole. In the young of all species and in the adults of *dimidiata, nasalis* and *bromeliacea*, the nostrils are very much enlarged. The carpals and tarsals are cartilaginous and there is a distinct sublingual fold below the anterior part of the free tongue.

The muscles and muscle patterns show specializations not seen in other Mexican and Central American genera. The intermandibularis anterior and hyoglossus are proportionally larger and more specialized than in other genera. The extent of these and other modifications will be indicated as the individual muscles are described.

TRANSVERSE THROAT MUSCLES

M. intermandibularis anterior (pl. LXVIII, fig. A; pl. LXIX, figs. A, D, G, H & J).

The origin of the muscle is in a small narrow strip of fascia, deep to the anterior slip of the intermandibularis posterior. The fascia extends laterally to attach to the dorsomedial surface of the mandible together with the fibers of the anterior slip of the posterior muscle. The shape of the muscle varies among the several species. In *multidentata, terrestris, dimidiata,* and *xolocalcae* it is triangular with the median angle extending as a wedge between the two opposing slips of the intermandibularis posterior; the anterior edge of the muscle is only slightly convex, in fact it is nearly transverse. In *arborea, nasalis, chiroptera, chondrostega,* and *lavae*, the muscle is expanded at the mid-ventral line but does assume a triangular shape. In this latter group the anterior edge of the

muscle may vary from concave as observed in *chondrostega* to convex in *chiroptera*. More important is its relatively large size in this genus. In typical *Chiropterotriton* this muscle reaches perhaps a higher state of development than in any genus in the family Plethodontidae.

In *abscondens*, the intermandibularis anterior has been completely lost. Because of this loss and other rather different variations to be considered later I have come to consider *abscondens* as an atypical species, which is myologically rather widely separated from the more typical forms of the genus.

M. intermandibularis posterior (pl. LXVIII, fig. A; pl. LXIX, figs. A, D, G, H, J & K).

The *anterior slip* originates along the dorsomedial surface of the mandible and the anterior margin is approximately one third of the length of the mandible posterior to the symphysis. The width of the origin varies from .3 to 1 mm, within the genus depending on the size of the individuals which make up the species. In *abscondens* the origin is .6 mm wide and is proportionally wider than in specimens of *terrestris, lavae, chondrostega* and *xolocalcae*, all of which have approximately the same snout to vent lengths (25-28 mm) and in which this muscle has a width at the origin of only .45 to .5 mm.

The muscle extends fanwise to the insertion in the ventral fascia with the most anterior fibers reaching the mid-ventral line, except in *abscondens* where they are just short of the line.

In all species, except *abscondens*, the anterior fibers extend from the origin to the insertion in a caudomedial direction. In *abscondens* the anterior fibers extend in an anteromedial direction and have come to occupy much of the area taken up by the anterior muscle in other species. This apparent anterior shift may serve to compensate for the loss of the intermandibularis anterior. Obviously the shift has increased the size of the muscle and, as in the case of its origin, substantially increased the proportional width of the insertion, when compared with other species. The slip in *abscondens* is therefore a much different muscle than it is in other *Chiropterotriton*.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible. The insertion is a broad fan in the ventral aponeurosis, between the anterior slip and the quadratopectoralis muscle. None of the fibers reach the mid-ventral line.

In *abscondens*, the fibers are relatively shorter and the line of insertion is longer than in other species.

M. gularis (pl. LXIX, figs. A, D, G, H, J & K).

The origin of this muscle is entirely in fascia. Approximately the anterior half arises from a thin aponeurosis, which is attached to the lateral edge of the mandible, to the quadrate and squamosal between the MM. depressor mandibulae and capiti mandibularis, to the caudolateral edge of the otic capsule and caudally along the fascia cephalodorsalis. In *abscondens* and *nasalis* the aponeurosis is attached high on the quadrate and is not attached to the mandible. In the two latter species the gularis is posterior to the tip of the mandible exposing clearly the entire insertion of the depressor mandibulae. In *xolocalcae* and *multidentata* the ventral portion of the insertion of the depressor mandibulae is exposed but in these forms it is not clearly shown. The insertion of the gularis is primarily on the skin of the gular fold. In all species there are a few anterior fibers inserted along the linea alba.

M. depressor mandibulae anterior (pl. LXIX, figs. A, G & K).

The anterior muscle originates chiefly on the squamosal and the lateral edge of the otic capsule. In a few species, *xolocalcae* for example, the most anterior fibers arise from the posterior edge of the quadrate. The most dorsal (otic) part is always deep to the cucularis major. The insertion is on the dorsal surface of the posterior tip of the mandible.

M. depressor mandibulae posterior (pl. LXIX, fig. K).

The posterior muscle originates in the fascia cephalordorsalis deep to the posterior part of the gularis. The insertion is on the ventral surface of the posterior tip of the mandible.

M. quadrato-pectoralis (pl. LXIX, figs. A, D, G, H, J & K).

The origin of the muscle is usually on the posterior edge of the quadrate and the squamosal. The large part is attached to the squamosal, in *xolocalcae*, *dimidiata* and *abscondens*. In the latter three species I could find no fibers arising from the quadrate. In *abscondens*, the origin is definitely attached only to the squamosal. The insertion is in the ventral aponeurosis between the intermandibularis and the gularis. None of the fibers reach the mid-ventral line although in *abscondens* the posterior ones are just short of reaching the gular fold. In all species, except *abscondens*, the insertion of the most anterior fibers is deep to the intermandibularis posterior.

M. interhyoideus (pl. LXIX, figs. A, D, H & K).

The origin of the muscle is on the anteroventral edge of the

ceratohyal approximately midway between its attachment on the squamosal and its sharp curve posterior to the tip of the articulare. The origin is clearly separated from the quadrato-pectoralis in all species. The insertion is in the ventral fascia deep to the anterior edge of the quadrato-pectoralis and the posterior part of the intermandibularis posterior. In *arborea, terrestris,* and *chiroptera* the insertion is entirely dorsal to the intermandibularis.

THE LONGITUDINAL AND DEEP MUSCLES

M. geniohyoideus medialis (pl. LXVIII, fig. A; pl. LXIX, figs. G, J & K; pl. LXXI, fig. D).

The origin of this muscle is on the posterior surface of the mandible immediately lateral to the symphysis. The width of the origin varies between .4 and .7 mm. The insertion is on the ventral surface of the subarcualis rectus 1 and along the anterior edge of the inscriptio tendinis but not extending to the mid-ventral line. The insertion is proportionally narrowest in *multidentata* and widest in *chondrostega* and *chiroptera.* In all species the lateral part of the muscle inserts caudal to the posterior tip of the mandible.

M. geniohyoideus lateralis (pl. LXVIII, figs. A & B; pl. LXIX, figs. G, J & K; pl. LXXI, fig. D).

The origin of the muscle is on the posterior and medial surfaces of the mandible, lateral to the medialis, except in *nasalis,* in which the medial fibers are dorsal to the medialis. In *arborea, xolocalcae, nasalis* and *abscondens* this muscle is divided near its origin by the anterior slip of the intermandibularis posterior and the intermandibularis anterior and there is a short distance between the two parts. In these species the largest part of the muscle arises on the medial edge of the mandible posterior to the anterior slip of intermandibularis posterior. In *dimidiata, chondrostega, lavae* and *multidentata* a few of the lateral fibers arise from fascia on the floor of the mouth immediately mediad and caudad to the origin of the anterior slip of the intermandibularis posterior. In *lavae* the fibers extend almost to the mandible.

The insertion is on the lateral edge of the ceratohyal, beginning medial to the posterior tip of the mandible, or slightly posterior to it in some species, and extending anteriorly approximately to the middle of the ceratohyal.

There appears to be a correlation between the extent of the development in the length of the origin of this muscle and the degree to which the species have attained aboreal habits. In *chiroptera* and *terrestris,* two entirely terrestrial species, the origin is com-

pletely anterior to the origin of the anterior slip of the intermandibularis posterior. An intermediate group composed of *dimidiata, chondrostega* and *multidentata* have the lateral fibers arising in fascia posterior to the mandible and medial to the origin of the intermandibularis muscles. These species are, according to the few sketchy reports dealing with them, mainly terrestrial. The species *lavae* can best be considered alone since it is mainly arboreal and has the origin of the lateral fibers reaching nearly to the mandible posterior to the intermandibularis. In the wholly arboreal species, (*arborea, xolocolcae* and *nasalis*) this muscle attains its greatest extent of attachment with approximately two thirds of the muscle arising on the mandible posterior to the anterior slip of the intermandibularis posterior. I have not seen *bromeliacia* but since it is entirely arboreal and closely related to *nasalis* (Schmidt 1936), I suspect that as regards this character, it will be the same as in *nasalis*. The habits of *abscondens* are not fully known. The few specimens collected were found under the bark of old stumps. The muscle arrangement and the attachment to the mandible in *abscondens* is similar to that in arboreal species, except that the part of the muscle arising posterior to the anterior slip represents only approximately half instead of two thirds of the origin.

M. rectus cervicis superficialis (pl. LXVIII, fig. A; pl. LXXI, fig. D).

The origin of the muscle is on the anterolateral edge of the sternum in all species. The fibers extend anteriorly and anterolaterally to cover completely the profundus at the first myocomma. From this point anteriorly the muscle is inseparably fused with the profundus. The insertion is with the profundus and will be described with the insertion of the following muscle.

M. rectus cervicis profundus (pl. LXVIII, fig. A; pl. LXXI, fig. D).

The major portion of this muscle is a direct continuation of the rectus abdominis. A small medial part arises from the lateral and anterolateral edge of the sternum, the more medial of which are deep to the superficialis. The insertion begins on the median surface of the subarcualis rectus 1 and extends medially along the inscriptio tendinis to the mid-ventral line. The insertion is in an irregular diagonal line.

The muscle is composed of three segments of unequal length; the posterior segment is approximately as long as the combined length of the other two; the middle segment is the shortest. The medial fourth of the anterior segment extends deep to insert on the floor of the mouth a short distance posterior to the suprapeduncu-

laris. In *Chiropterotriton* this slip is narrow and the fibers converge at the insertion.

M. rectus cervicis lateralis (as in pl. LXXI, figs. C & E).

The origin of this muscle is on the lateral edge of the sternum or on the myocomma immediately lateral to the sternum. The Insertion is in fascia which is on the lateral surface of the abdominohyoideus at approximately the level of the thyroid gland.

This muscle occurs in all species, except *nasalis* where it is apparently not present, at least not in the single specimen examined. It is an extremely small muscle throughout the entire genus, reaching its largest size in *chiroptera.* It was readily discernible in the very small *dimidiata.*

M. subarcualis rectus 1 (pl. LXVIII, fig. A; pl. LXXI, fig. D; pl. LXXIII, fig. C).

The origin of the muscle is on the ventral surface of the ceratohyal, beginning at the base of its anterior blade and extending caudad along its lateral edge to a point medial to the posterior tip of the mandible or slightly posterior in some species. A shorter row of fibers arises along the medial edge of the ceratohyal. The insertion begins near the mid-ventral line and extends laterally along the inscriptio tendinis to the distal ends of the ceratobranchials and the tendinous sheath surrounding the epibranchial. The muscle extends caudally at least to the posterior margin of the front leg in all species. It is proportionally shortest in *chondrostega* and longest in *xolocalcae.* In *nasalis, arborea, multidentata* and *abscondens* it is relatively elongate.

M. suprapeduncularis (pl. LXVIII, fig. B; pl. LXXIII, fig. C).

This muscle is attached to the dorsomedial surface of the ceratohyals beginning at the base of the anterior blade and extending caudad to the point at which the ceratohyals curve laterad. There are no transverse pharyngeal fibers posterior to it, except in *abscondens.* In this genus the suprapeduncularis is relatively uniform in size and shape.

M. hyoglossus (pl. LXVIII, fig. C).

The muscle arises on the ventral surface of the anterior tip of the basibranchial. From the origin the fibers extend fanwise anterodorsally to insert in the tissue of the tongue.

The ventral origin of the hyoglossus is peculiar to the genus *Chiropterotriton* and may be used as a reliable generic character.

In the genus *Chiropterotriton* the anterior part of the ceratohyal is curved ventrally around the stalk of the tongue and terminates

anterior to the suprapeduncularis in a narrow blade. The thin medial edges of the two opposing "blades" are almost in contact at the linea alba. The exception to this is in *abscondens,* in which the ceratohyal terminates in a round attenuated rod of cartilage, with no suggestion of a flattening of the proximal ends.

SUMMARY

The genus *Chiropterotriton* has undergone adaptive specializations to such an extent that it is now possible, on the basis of the throat myology and the nature of the ceratohyals, to arrange the species into three groups. The groups are not of equal taxonomic value and are established for the express purpose of indicating the specific and intra-specific variations extant in the genus.

Group I		
chiroptera	*dimidiata*	(*mosaueri*)
terrestris	*multidentata*	
chondrostega	*lavae*	
Group II		
arborea	*nasalis*	
xolocalcae	(*bromeliacia*)	
Group III		
abscondens		

Species in parenthesis were not seen, and their position is tentative.

The species of group I are, on the basis of muscle patterns, the most generalized of the genus. The geniohyoideus has not become specialized, and the subarcualis rectus 1 is relatively shorter than in either of the other groups. The muscles appear to be least specialized in *chiroptera* and *chondrostega* and most specialized in *lavae.* The most generalized form in this group appears to be *chiroptera,* which may represent the nearest link to the ancestor of the genus. I am inclined toward the opinion that the ancestors of these salamanders were entirely terrestrial in their habits.

In group II the species are entirely arboreal in habit, and all have a highly specialized geniohyoideus lateralis and a much longer subarcualis rectus 1. The real reason for these specializations is unknown to me, but I suspect them to be correlated with changes in feeding habits and possibly with their behavior associated with climbing. Aside from these differences, the species of group I and II are similar and together form a closely related series of species developed as a result of adaptive radiation.

The single species in group III is more closely related to the

aboreal species of group II than to those group I. This relationship does not appear to be close, however, for I can recognize no close relatives among the assemblage of known species. It should be pointed out, however, that *abscondens*, in spite of its attenuated ceratohyals and missing intermandibularis anterior, is not an annectant form relating, for example, *Thorius* with *Chiropterotriton*. The muscle patterns, unquestionably those of a *Chiropterotriton*, have been modified from the general muscle patterns of the genus, because of specializations brought about by its changing habits, habitats, or more probably both. The entire external anatomy, the shape of the feet and the hands, the dental patterns, the shape of the snout, and the absence of an orbitolabial groove all testify to its proper association with *Chiropterotriton*.

GENUS *Parvimolge* Taylor

Parvimolge Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, no. 12, 1944, p. 223 (type *Oedipus townsendi* Dunn).

The genus *Parvimolge* includes only two known species of diminutive terrestrial salamanders. *P. townsendi* inhabits parts of Central Mexico while *P. richardi* is known only from Costa Rica. The following characteristics will distinguish them from any other Mexican or Central American salamanders. The middle digits are only approximately half webbed, with the distal half of each free and with the tips pointed. The middle toe and second finger are considerably longer than other adjoining digits. There is a sublingual fold present and the maxillary is toothed. The skull is well ossified; the carpals and tarsals are cartilaginous and the nasals are enlarged.

The following descriptions of the throat musculature and the hyobranchial cartilages will indicate certain of the anatomical conditions existing in this genus and will add to the known list of distinguishing characteristics.

The descriptions are based entirely on the throat anatomy of *townsendi*, except for a few characters which could be noted without dissecting the type specimen of *richardi*.

THE THROAT MYOLOGY AND THE HYOBRANCHIAL APPARATUS

TRANSVERSE THROAT MUSCLES

M. intermandibularis anterior (pl. LXIX, fig. F).

The origin of the anterior muscle is in fascia deep to the anterior margin of the anterior slip of the intermandibularis posterior. The fascia extends lateral in conjunction with that of the anterior slip and is attached to the dorsomedial surface of the mandible. The

muscle is narrow, approximately .2 mm wide at the mid-ventral line and is .3 mm posterior to the symphysis. There is no sign of a median raphe.

M. intermandibularis posterior (pl. LXIX, fig. F).

The *anterior slip* originates on the dorsomedial surface of the mandible approximately .9 mm caudolateral to the symphysis. The insertion is in the ventral aponeurosis and anteriorly along the mid-ventral line. The latter represents about one fourth of the slip.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible. The insertion is in the ventral fascia. The median fibers are longest but do not extend to the mid-line.

Both slips have extensive insertions and are broadly fan-shaped, together they cover most of the area between the mandibles.

M. gularis (pl. LXIX, fig. F).

The origin of the gularis is in fascia; the anterior part arises from a thin sheet of fascia which is attached to the lateral surface of the posterior tip of the mandible, the quadrate, the squamosal and the otic capsule; the posterior part arises in the fascia cephalodorsalis. The insertion is on the gular fold except for a small anterior portion which inserts along the mid-ventral line. The posterior tip of the mandible is deep to this muscle.

M. depressor mandibulae anterior.

The anterior muscle arises from the squamosal and the otic capsule. The M. cucularis major arises from the skull along the caudal and dorsal edges of this muscle, and is not superior to the otic part of the depressor mandibulae as it is in most other genera. The insertion is on the dorsal surface of the posterior tip of the mandible.

M. depressor mandibulae posterior.

The posterior muscle arises along the fascia cephalodorsalis deep to the gularis and superior to the cucularis. The origin is extensive and reaches the gular fold. The insertion is ventral to the anterior muscle. Both muscles are large and distinctly separated.

M. quadrato-pectoralis (pl. LXIX, fig. F).

The origin of this muscle is on the posterior edge of the squamosal and on the ventral edge of the ligament attaching the ceratohyal to the squamosal. There are no fibers attached to the quadrate in the specimen examined. The insertion is in the ventral aponeurosis between the intermandibularis posterior and the gularis.

M. interhyoideus.

The origin of the interhyoideus is on the anteroventral surface of

the distal end of the ceratohyal. The insertion is in the ventral aponeurosis, deep to the intermandibularis posterior and the quadrato pectoralis. The larger part, comprising approximately two-thirds of the muscle, is deep to the intermandibularis.

THE LONGITUDINAL AND DEEP MUSCLES

M. geniohyoideus medialis (pl. LXX, fig. E; pl. LXXII, fig. E). The origin of the medialis is on the posterior surface of the mandible beginning at the symphysis and extending laterad for approximately .4 mm. The lateral part of the muscle inserts on the ventral surface of the subarcualis rectus 1. The medial part is attached to the anterior edge of the inscriptio tendinis, but does not extend to the mid-ventral line. The insertion forms a diagonal line, with the lateral portion extending posteriorly to a line between the caudal tips of the mandible. The muscle is rather uniform in width and is only slightly wider near the insertion than at the origin.

M. geniohyoideus lateralis (pl. LXX, fig. E; pl. LXXII, fig. E). The origin of the lateralis is on the posterior surface of the mandible lateral and dorsal to the medialis. The origin of the lateralis does not extend to the anterior slip of the intermandibularis posterior, and there are no fibers arising in fascia laterad or caudad to the anterior slip. The insertion is on the lateral edge of the ceratohyal beginning approximately at the level of the posterior tip of the jaw and extending anteriorly for about .9 mm.

M. rectus cervicis superficialis (pl. LXX, fig. E; pl. LXXII, fig. E). The origin of this muscle is on the anterolateral edge of the sternum. The lateral edge of the origin is approximately half way between the mid-line and the lateral edge of the profundus. The superficialis does not reach to the lateral edge of the profundus at the first myocomma anterior to the sternum, but is closely applied to the profundus anterior to the first myocomma. The insertion is with the profundus.

M. rectus cervicis profundus (pl. LXX, fig. E; pl. LXXII, fig. E). The major portion of this muscle is a direct continuation of the rectus abdominis. A small medial portion arises from the sternum lateral and dorsal to the superficialis. The insertion is on the ventral surface of the subarcualis rectus 1, directly caudad to the geniohyoideus medialis, and extends medially along the inscriptio tendinis to the mid-ventral line. The posterior segment is approximately as long as the combined length of the two anterior segments; the most anterior segment is the shortest. The deep slip of the rectus cervicis is attached to the medial part of the anterior

myocomma and is entirely deep to the superficial part of the muscle. This slip is inserted on the floor of the mouth posterior to the suprapeduncularis.

M. rectus cervicis lateralis (as in pl. LXXI).

The lateralis is present as a very fine bundle of fibers arising from near the extreme lateral edge of the sternum and extending anterolaterad to the lateral surface of the abdominohyoideus. How far it extended anteriorly could not be determined.

M. subarcualis rectus 1 (pl. LXX, fig. E; pl. LXXII, fig. E).

The origin of this muscle is on the ventrolateral and ventromedial edges of the ceratohyal. The lateral part begins with the medial part at the base of the anterior "spade" of the ceratohyal, and extends posteriorly approximately to the level of the caudal tip of the mandible, whereas the medial part extends for only about half that distance along the medial surface. The insertion extends along the inscriptio tendinis, to the distal ends of the ceratobranchials and extends posteriorly along the tendinous sheath surrounding the epibranchial.

The muscle is proportionally longer in both species of *Parvimolge* than it is in any species of *Chiropterotriton* save *C. xolocalcae* in which it is approximately of the same relative length.

M. suprapeduncularis (pl. LXX, fig. E).

The origin of the suprapeduncularis is on the dorsomedial surface of the ceratohyals, beginning at the base of the enlarged anterior spade of the ceratohyal, which is approximately .4 mm from the anterior end, and extending caudad for about .5 mm. The anterior fibers are approximately a third longer than those near the posterior end. The muscle is widely separated from the deep slips of the rectus cervicis. The muscle resembles very closely that found in the genus *Chiropterotriton* and some *Pseudoeurycea*.

M. hyoglossus.

The origin of the hyoglossus is on the anterior edge of the basibranchial between the short anterolaterally projecting cornua. The insertion is in the anterior semicircle of the tongue anterodorsal to the origin.

The ceratohyals are similar in shape and size to those found in *Chiropterotriton* and *Pseudoeurycea*. They are peculiar in that the anterior lobes are considerably overlapped along the mid-ventral line and the medial lobes are widely separated. The other hyobranchial cartilages are not variable.

GENUS *Magnadigita* Taylor

Magnadigita Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, 1944, pp. 189-232 (type *nigroflavescens*).

The genus *Magnadigita* includes at least fifteen species of medium to large terrestrial and arboreal salamanders. They range over the greater part of Central America and have entered southern Mexico and northern South America. The members of this genus are readily distinguished from all other genera by the complete absence of the sublingual fold and by having the tips of the digits truncate and the distal part of the digits free from webbing. This combination of characters is singular to the genus *Magnadigita* and together may be used as an easy method of recognizing the species of the genus. The habitats of the several species are rather variable, some being found in and under old logs, others in bromelias and some living under rocks and in live moss. The genus *Magnadigita* has seemingly undergone adaptive radiation in much the same way as have other large genera such as *Pseudoeurycea* and *Chiropterotriton* with the resulting large series of distinct and diversified species.

The following myological descriptions will indicate other less obvious characteristics of the genus.

THE THROAT MYOLOGY AND THE HYOBRANCHIAL APPARATUS

TRANSVERSE THROAT MUSCLES

M. intermandibularis anterior (pl. LXX, fig. C).

The origin of the anterior muscle is in fascia at the anterior edge of the anterior slip of the intermandibularis posterior. The medial and posterior fibers arise deep to the anterior slip. This muscle is absent in *robusta* and *subpalmata*. In *engelhardti* and *dunni* the muscle is very narrow being less than .2 mm wide in *engelhardti;* it is widest in *franklini* (.4 mm) and is well developed in *rostrata* and *macrinii*. This muscle is noticeably shorter than it is in other genera, having in *dunni*, a length of scarcely more than 1 mm. In *nigroflavescens* this muscle is inserted at the median raphe there being no fibers which are continuous across the mid-ventral line.

In *nigroflavescens* this muscle is completely divided and is inserted in fascia at or lateral to the mid-ventral line. Besides the variable sizes and conditions existing in this muscle, is the fact that in all species it is relatively small in size.

M. intermandibularis posterior (pl. LXX, figs. B & C).

The *anterior slip* originates on the dorsomedial surface of the mandible, approximately one third of the length of the mandible

posterior to the mental symphysis. The insertion is in the ventral aponeurosis caudomedial to the origin. In *subpalmata, franklini* and *macrinii* the most anterior fibers reach the mid-ventral line, in all others the insertion is lateral to the mid-line. In some species approximately one third or more of the muscle arises from fascia extending from the mandible mediad along the edge of the anterior slip.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible. The insertion is in the ventral aponeurosis between the anterior slip and the quadrato-pectoralis. The posterior fibers are inserted anterior to a line between the posterior tips of the mandibles and there is a greater distance from the tip of the mandible to the origin of the most caudad fibers, than is commonly found in other genera.

M. gularis (pl. LXX, figs. B & C; pl. LXXII, fig. G).

The origin of the gularis is in a thin sheet of fascia, which is attached to the mandible and dorsad along the quadrate and squamosal to the lateral edge of the otic capsule. Posterior to the otic capsule the fibers arise directly from the fascia cephalodorsalis, thus eliminating the aponeurosis. A few of the superficial fibers arise from the skin. The insertion is on the skin of the gular fold and medially along the linea alba. A few of the anterior fibers of the muscle are inserted at the mid-ventral line, except in *robusta,* and the posterior tip of the mandible is always deep to the anterior edge of this muscle.

M. depressor mandibulae anterior.

The anterior muscle originates on the squamosal and the lateral edge of the otic capsule. Only the posterior fibers of the muscle arise from the otic capsule and these are deep to the cucularis major in all species except *robusta.* The insertion is on the dorsal surface of the posterior tip of the mandible.

M. depressor mandibulae posterior.

The posterior muscle originates in the fascia cephalodorsalis deep to the gularis. It does not extend caudad to the gular fold and is approximately the same size as that of the anterior muscle. The insertion is ventral to the insertion of the anterior muscle.

M. quadrato-pectoralis (pl. LXX, figs. B & C).

The origin of this muscle in *Magnadigita* is rather irregular and cannot be described in a single statement. In *macrinii, franklini, engelhardti* and *subpalmata* this muscle arises from the squamosal and the tendinous tissue attaching the ceratohyal to the skull. In

other species the fibers arise from the quadrate, squamosal and from the tendinous tissue, although the proportions of origin vary considerably with most of the fibers arising from the squamosal in *rostrata* and with a greater part originating on the quadrate in *robusta*. The origin appears to be determined, in part at least, by the point of attachment of the ceratohyal on the squamosal, at least on the relative distance from the attachment to the dorsal tip of the quadrate. If the ceratohyal is attached near the dorsal tip of the quadrate and the most caudoventral edge of the squamosal, as in *robusta*, then much of the muscle arises from the quadrate. The origin is always in the angle between the ceratohyal and the skull, with at least one fourth of the muscle arising from the tendinous tissue around the ceratohyal and with the remainder arising from either the squamosal or from both the squamosal and the quadrate.

The insertion is in the ventral aponeurosis, the anterior fibers are deep to the intermandibularis posterior and in *robusta* and *macrinii* the posterior fibers extend to the gular fold and at that point reach the linea alba.

M. interhyoideus (pl. LXX; figs. B & C).

The origin of the interhyoideus is on the anteroventral surface of the ceratohyal between the outer edge of the curve in the ceratohyal caudad to the posterior tip of the jaw and its attachment to the squamosal. The insertion is in the ventral aponeurosis deep to the posterior slip of the intermandibularis posterior. In *robusta* and *nigroflavescens* the posterior part of this muscle is deep to the quadrato-pectoralis.

THE LONGITUDINAL AND DEEP MUSCLES

M. geniohyoideus medialis (pl. LXXIV, fig. E).

The origin of the medialis is on the posterior margin of the mandible, beginning at the symphysis and extending laterad for more than half the distance from the symphysis to the origin of the anterior slip of the intermandibularis posterior. The insertion is on the ventral surface of the subarcualis rectus 1 and medially along the anterior edge of the inscriptio tendinis but not extending to the mid-ventral line. The medialis is a straplike muscle not greatly expanded at the insertion and with its margins reasonably straight. The insertion is usually posterior to the tip of the mandible.

M. geniohyoideus lateralis (pl. LXXII, fig. G; LXXIV, fig. E).

The origin of the lateralis is on the posterior margin of the mandible dorsal and lateral to the medialis, except in *rostrata* where it is entirely lateral. The insertion is on the lateral edge and the

dorsal surface of the ceratohyal beginning at, or slightly posterior to, a point caudad to the tip of the mandible and extending anteriorly to approximately the middle of the ceratohyal.

M. rectus cervicis superficialis.

The origin of this muscle is on the anterolateral edge of the sternum. The insertion is with the profundus at the inscriptio tendinis. In *robusta, nigroflavescens, subpalmata* and in an undescribed species the lateral fibers extend completely to the lateral margin of the profundus at the first myocomma anterior to the sternum. In the other species seen, the superficialis does not reach to the lateral margin of the profundus.

M. rectus cervicis profundus.

The profundus is an anterior extension of the rectus abdominis except for a few medial fibers which arise from the sternum. The insertion is on the ventral surface of the subarcualis rectus 1 and medially along the posterior edge of the inscriptio tendinis to the mid-ventral line. The muscle is divided into three segments. The posterior portion is the longest but is less than half the length of the entire muscle. The medial fibers of the anterior segment extend deep to the abdominohyoideus and the second ceratobranchial and are inserted on the floor of the mouth in all species except *macrinii* in which the lateral fibers extend to the ceratohyals, (pl. LXXII, fig. G; pl. LXXIII, fig. D; pl. LXXIV, fig. E). A series of short pharyngeal fibers extends from the insertion of the deep slip to the posteromedial edge of the ceratohyals. The anterior fibers form continuous caudal loops between the ceratohyals, but are not extended anteriorly between the closely approximating medial lobes of the ceratohyals.

M. rectus cervicis lateralis.

The origin of the lateralis is on the most lateral border of the sternum immediately lateral to the superficialis. It extends diagonally across the profundus to the lateral surface of the abdominohyoideus where it is inserted in fascia at the level of the thyroid gland. This muscle was not present in single specimens of *subpalmata* and *engelhardti.*

M. subarcualis rectus 1 (pl. LXXII, fig. G).

The origin of this muscle is on the ventral surface of the ceratohyal, beginning medially a short distance from the anterior end of the ceratohyal and extending caudad and caudolaterad approximately to the level of the posterior tip of the mandible. The fibers do not arise along the medial border as observed in other genera, but are near the center and along the lateral edge. The insertion

is along the anterior edge of the inscriptio tendinis, deep to the lateral half of the geniohyoideus medialis, on the distal ends of the ceratobranchials and along the tendinous sheath surrounding the epibranchial. The muscle is long and extends several millimeters caudad to the posterior border of the front leg in all species.

M. suprapeduncularis (pl. LXXII, fig. G; pl. LXXIII, fig. D; pl. LXXIV, fig. E).

The fibers of the suprapeduncularis arise from the dorsomedial surface of the ceratohyal, beginning immediately posterior (approximately .5 mm.) to the anterior end of the ceratohyal and extending caudad for 1 or 2 mm. depending on the size of the specimen. The fibers are continuous between the ceratohyals and become progressively shorter from anterior to posterior. The muscle is much wider than long and appears as a smaller V-shaped muscle anterior to the medial lobes of the ceratohyals. The suprapeduncularis is distinctly separated from the pharyngeal muscles and the deep slip of the rectus cervicis by an elongate narrow space extending caudad from the suprapeduncularis between the medial lobes of the ceratohyals.

M. hyoglossus.

The origin of the hyoglossus is on the anterior tip of the basibranchial between the elongate cornus. The fibers extend fanwise and are inserted in the anterior tissues of the tongue.

VARIATIONS IN THE HYOBRANCHIAL APPARATUS

In all *Magnadigita* the cornua of the first basibranchial are greatly elongated, being at least 1 mm. long in all species and in the larger species nearly 2 mm. The cornua extend anterolaterad from the basibranchial and are curved to nearly an anterior position at the tips.

The proximal ends of the ceratohyals terminate in blunt or rounded points only a short distance beyond the origin of the suprapeduncularis muscle. The anterior medial margins are straight and are directed slightly mediad so that a deep V-shaped space, partially occupied by the suprapeduncularis, is formed. The concavity present along the medial margins in other genera is indicated only in *robusta.* Furthermore the space separating the ceratohyals posterior to the suprapeduncularis muscle is extremely narrow in all species except *dunni.* The ceratohyals are widest near the posterior edge of suprapeduncularis and are narrow and attenuated distally. Posterior to the angle of the jaws, the ceratohyals curve at less than a ninety-degree angle, and their most distal tip is attached to the squamosal by a ligamentous sheath.

SUMMARY

An attempt to establish, on the basis of the throat masculature and the hyobranchial cartilages, an intrageneric relationship of the species of this genus would be most difficult. The muscles and muscle patterns as well as the size and shape of the ceratohyals are rather uniform. However, I have come to regard *robusta* as the most primitive of the species, mainly because of the primitive origin of the quadrato-pectoralis and the presence of a large mass of pharyngeal fibers between the anterior ends of the deep slip of the rectus cervicis and the suprapeduncularis muscles. The fact that it is a terrestrial species also suggests a primitive status. The species *subpalmata* is also a generalized one, but is more specialized than *robusta*. The muscle patterns of *engelhardti, nigroflavescens, dunni,* and *franklini* are similar and represent the most specialized forms of the genus. Together these four form a series of closely related species, of which *engelhardti,* with its narrow specialized intermandibularis anterior and with the origin of the quadrato-pectoralis entirely free of the quadrate, is the most specialized.

The intermandibularis anterior is extremely variable in this genus; it is probably in the process of becoming reduced and may eventually be lost to the species of this genus.

The GENUS *Bolitoglossa* Duméril and Bibron

Bolitoglossa Duméril and Bibron, 1854, Erpétologie général de l'histoire naturelle complete des Reptiles. vol. IX, p. 88. (type *mexicana*).

The genus *Bolitoglossa* includes the largest series of species of any of the Mexican and Central American genera. In all there are at least twenty-five species, three of which are as yet undescribed. The species are adapted mainly for arboreal life but some are known to live on the ground and under rocks.

The greater number of known species inhabit Mexico and Central America but some are also known from South America, giving the genus a very extensive range.

The species belonging to the genus *Bolitoglossa* are readily distinguished from all other plethodontids by the presence of a heavy glandular webbing on the hands and feet, from which only the tips of the middle digits may be free, giving to both hands and feet a palmate appearance. They are also characterized by the complete absence of the sublingual fold.

The following description of the hyobranchial apparatus and its musculature will set forth the myological characteristics of the genus.

THE TRANSVERSE THROAT MUSCLES

M. intermandibularis anterior (pl. LXX, figs. G, H, I & J).

The origin of this muscle is variable; in *rufescens* and *striatula* the fibers arise from fascia immediately medial to the mandible, while in other species studied the fibers arise from fascia along the anterior edge of the anterior slip of the intermandibularis posterior. In *rufescens* and *striatula* the fibers are nearly parallel to those of the anterior slip of the intermandibularis posterior, but are easily distinguished by the absence of the median raphe. In an undescribed species from Costa Rica, the muscle is completely divided at the mid-ventral line. The muscle is small in all species and may vary considerably among the individuals of a species. In three specimens of *flaviventris*, the size (width) ranged from an extremely small narrow muscle to one as large as any observed in other species of the genus. This muscle may be absent in some species.

M. intermandibularis posterior (pl. LXX, figs. G, H, I & J).

The *anterior slip* originates on the dorsomedial surface of the mandible approximately one third of the length of the mandible from the symphysis. The insertion is in the ventral aponeurosis lateral to the mid-ventral line in all species examined. In *rufescens* and *striatula*, the anterior fibers extend only slightly more than half way to the mid-ventral line, whereas in *occidentalis* the fibers extend nearly to the mid-line. The line of insertion may be convex as in *rufescens*, straight as in *striatula*, concave as in *occidentalis*, or irregular as in *flaviventris*. In one specimen of the last species there is a middle slip extending mediad from its origin on the dorsal surface of the mandible between the two normal slips. It is inserted in the ventral fascia. The anterior part is deep to the anterior slip and the posterior part superficial to the posterior slip. This is another example of the variation obtaining in *flaviventris*.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible. The insertion is in the ventral aponeurosis. The muscle is fan-shaped and extends as far medially as the fibers of the anterior slip. The posterior fibers are nearly transverse and are inserted anterior to a line between the posterior tips of the mandibles.

M. gularis (pl. LXX, figs. G, H, I & J).

The origin of the gularis is entirely in fascia, the anterior portion arising from a thin aponeurosis which is attached to the lateral edge of the mandible and extends dorsad along the quadrate, squamosal and the lateral margin of the otic capsule. The posterior portion arises from the fascia cephalodorsalis and from the skin superior and dorsomedial to the fascia. The greater part of the insertion is on the skin of the gular fold, but approximately one third of the insertion is on the linea alba. No fibers reach the mid-ventral line; however, in most species the opposing gularis muscles are separated only by a distance of about one millimeter. The posterior tip of the mandible is always covered by the gularis.

M. depressor mandibulae anterior (pl. LXXII, fig. I).

The anterior muscle originates on the squamosal and the caudolateral edge of the otic capsule immediately dorsal to the squamosal. The part arising from the otic capsule is usually deep to the cucularis major. The insertion is on the dorsal half of the posterior tip of the mandible.

M. depressor mandibulae posterior (pl. LXXII, fig. I).

The posterior muscle originates in the fascia cephalodorsalis deep to the gularis. The insertion is on the ventral half of the posterior tip of the mandible.

M. quadrato-pectoralis (pl. LXX, figs. G, H, I & J).

This muscle arises in the angle formed by the attachment of the ceratohyal to the skull, being attached to the posterior edges of the quadrate and squamosal, and the ventral margins of the ceratohyal near its attachment to the skull. These surfaces are used in varying degrees by all species for the attachment of this muscle. In *platydactyla, flaviventris* and *mexicana* the dorsal tip of the quadrate gives rise to the majority of the fibers while in *rufescens* most of this muscle originates on the squamosal and there are no fibers attached to the quadrate. The tendinous mass around the ceratohyal gives rise to a small part of this muscle in all species. The insertion is in the ventral aponeurosis between the intermandibularis posterior and the gularis. A few of the anterior and posterior fibers are deep to the adjoining muscles.

The origin, insertion and shape of this muscle is reminiscent of the relations existing in the genus *Magnadigita*.

M. interhyoideus (pl. LXX, figs. G, H, I & J).

The origin of the interhyoideus is on the anteroventral surface of the ceratohyal between the attachment of the ceratohyal to the skull and the angle of the ceratohyal posterior to the caudal tip of the mandible. The insertion is in the ventral aponeurosis deep

to the intermandibularis posterior but with a few of the posterior fibers deep to the quadrato-pectoralis. The usual decussation of the fibers is present in all species.

THE LONGITUDINAL AND DEEP MUSCLES

M. geniohyoideus medialis (pl. LXXI, fig. B; pl. LXXII, fig. A).

The origin of the medialis is on the posterior edge of the mandible immediately lateral to the symphysis. In *striatula* the origin extends less than half the distance from the symphysis to the origin of the anterior slip of the intermandibularis posterior, whereas in *platydactyla* the origin extends for approximately three fourths of the distance. The insertion is lateral on the ventral surface of the subarcualis rectus 1 and medial along the inscriptio tendinis. The insertion does not extend to the mid-ventral line; it is however, very near the mid-line in *flaviventris* but fails to reach it by at least half its width in the other species. The lateral fibers are inserted at the level of the posterior tip of the mandible or posterior to it in all species.

M. geniohyoideus lateralis (pl. LXXI, fig. B; pl. LXXII, fig. A).

The origin of the lateralis is on the posterior edge of the mandible dorsal and lateral to the medialis. In *striatula* the entire muscle is lateral, while in *platydactyla* all except the most lateral fibers are dorsal to the medialis. These two species represent the extremes, the other species varying between them. It is only in *striatula* that the lateralis originates entirely dorsal to the medialis. The insertion is on the lateral and dorsal surface of the ceratohyal, beginning at the level of, or slightly caudad to, the posterior tip of the mandible and extending anteriorly approximately to the middle of the cartilage.

M. rectus cervicis superficialis (pl. LXXI, fig. B; pl. LXXII, fig. A).

The origin of this muscle is on the anterolateral edge of the sternum extending from the linea alba caudolaterad to the lateral tip of the sternum. The insertion is with the profundus and will be noted in the description of that muscle. In *Bolitoglossa* the superficialis is a rather narrow muscle and is medial to the lateral edge of the profundus in all species examined.

M. rectus cervicis profundus (pl. LXXI, fig. B; pl. LXXII, fig. A).

The greater part of this muscle is a continuation of the rectus abdominus, with only a small medial part arising from the lateral edge of the sternum. The insertion is on the ventral surface of the subarcualis rectus 1 and anteromedial along the posterior edge of the inscriptio tendinis to the mid-ventral line. This muscle is di-

vided by two myocommata into three unequal segments. In *rufescens, striatula* and *mexicana* the posterior segment is shorter than the combined lengths of the two anterior segments, in *flaviventris* it is approximately equal to the two anterior segments, and in *platydactyla, occidentalis* and two undescribed species it is longer. The medial fibers of the anterior segment extend deep to insert on the floor of the mouth a short distance posterior to the ceratohyals. Between the insertion and the ceratohyals is a short muscle appearing much the same as in *Magnadigita subpalmata.* The only exception is *rufescens* in which the intervening muscle fibers are absent and the deep slip is extended slightly more anteriorly than in other species.

M. rectus cervicis lateralis.

In spite of careful disections and observations of many species the lateralis muscle was seen only in *mexicana.* In large examples of both *platydactyla* and *flaviventris* not the slightest indication of it could be found. The origin in *mexicana* is on the extreme lateral edge of the sternum, noticeably lateral to the superficialis muscle. From the origin the fibers extend diagonally across the profundus and are inserted in fascia on the lateral surface of the abdominohyoideus near the level of the thyroid gland.

The lateralis muscle in *mexicana* is not particularly different from the lateralis of *Magnadigita* or *Pseudoeurycea.* The most important consideration lies in the fact it is absent from such a large segment of the genus *Bolitoglossa.*

M. subarcualis rectus 1 (pl. LXXI, fig. B; pl. LXXII, figs. A & I).

The origin of this muscle is on the ventral surface of the ceratohyal, beginning a short distance from the anterior end of the ceratohyal and extending posteriorly along the lateral and medial margins. The fibers along the lateral side of the ceratohyal extend farther posteriorly than do those on the medial edge, however in *Bolitoglossa* the difference is not nearly as great as in other genera. In *mexicana* the lateral row of fibers is interrupted by a short diastema in which no fibers are attached to the ceratohyal. In *rufescens* only a small posterior portion of the lateral row of fibers has been retained.

M. suprapeduncularis (pl. LXXIII, figs. A & F).

The origin of the suprapeduncularis is on the dorsomedial surface of the ceratohyals immediately caudal to their anterior tips. In size and shape this muscle is much the same as it is in *Magnadigita.* In *platydactyla* the posterior fibers are almost as long as

the anterior fibers and the muscle is divided into four rather distinct bundles. In an undescribed species from Mexico this muscle is very small and has been pushed anteriorly by the wide contact of the ceratohyals posterior to the muscle.

M. hyoglossus.

The origin is on the anterior margin of the tip of the basibranchial. The surface is between the cornua and does not extend to any part of the ventral surface. The origin and insertion of the hyoglossus and the length and shape of the cornua are very similar, even in details, to the conditions obtaining in the genus *Magnadigita.*

VARIATIONS IN THE HYOBRANCHIAL APPARATUS

The ceratohyals in *Bolitoglossa* are essentially the same as described for *Magnadigita.* In *rufescens* the shape and general appearance is similar, except that the entire hyobranchial structure is noticeably posterior to that of other species of *Bolitoglossa.*

SUMMARY

In *Bolitoglossa* the entire throat musculature and the hyobranchial skeleton are similar to the conditions found in *Magnadigita.* The main difference between the two genera lies in the absence of the rectus cervicis lateralis from the large majority of species of *Bolitoglossa.* The myology in both is generalized and compares rather well with many of the muscle patterns in the generalized species of the genus *Pseudoeurycea.*

The species *platydactyla* appears to be the most primitive of the genus *Bolitoglossa* at least among the species studied. The origin of the quadrato-pectoralis, the elongate posterior fibers of the suprapeduncularis, the unspecialized geniohyoideus muscles, and the large mass of pharyngeal muscles between the deep slip of the rectus cervicis and the suprapeduncularis mark it as primitive. The presence of the rectus cervicis lateralis in *mexicana* marks it as a primitive species, although I consider it to be more specialized than *platydactyla,* because of the reduced pharyngeal muscles and the smaller extent of the insertions.

The small *rufescens* is obviously the most specialized as well as the most aberrant species of the genus. The primary specializations of *rufescens* are to be found in the origin of the subarcualis rectus 1, in the origin of the quadrato-pectoralis on the squamosal and not on the quadrate, and in the noticeably posterior position of the ceratohyal. From the nature of the throat anatomy, *rufescens*

appears to be closely related to *striatula* and *occidentalis.* It may also be allied to *lignicolor* and *colonnea,* both of which are unknown to me.

There are obviously two major groups of species in the genus. The first includes the larger species, *platydactyla, flaviventris* and *mexicana;* and the second includes the smaller species *occidentalis,* two undescribed species, and possibly *rufescens.* The last species, although not entirely typical, does have many affinities to the species of the second group and is best placed with them rather than as a separate group. A rather noticeable difference between *rufescens* and other bolitoglossids is the more pointed nature of the jaws at the symphysis. In all other forms the jaws are much more rounded, even in species such as *occidentalis,* which appear to be most closely related to it.

The myology of *striatula* is not typical of either group. As regards the origin of the quadrato-pectoralis, it is like that of the first group, but in many other characters already noted, *striatula* is similar to *rufescens* or is unique as in the origin of the geniohyoideus lateralis.

GENUS *Oedipina* Keferstein

Oedipina Keferstein, Nachr. Ges. Göttingen, vol. 15, 1868, p. 331 (type *uniformis*).

The genus *Oedipina* includes at least ten species of greatly elongate, wormlike, terrestrial salamanders. They are characterized, by having small legs, a tail which is usually much longer than the combined length of the head and body; fully webbed digits with only the tips free and more or less pointed or rounded and by having seventeen to twenty costal grooves. The adpressed limbs are separated by half or more of the costal grooves present.

The following myological considerations are based almost entirely on *uniformis, complex, parvipes* and on two undescribed species. The types of *serpens* and *syndactyla* were seen, but were not dissected except to determine the origin of the M. geniohyoideus lateralis and the shape of the anterior part of the ceratohyals.

THE THROAT MYOLOGY AND THE HYOBRANCHIAL APPARATUS

TRANSVERSE THROAT MUSCLES

M. intermandibularis anterior (pl. LXX, fig. D).

The origin of this muscle is in a small flattened straplike fascia extending from the muscle laterad to attach to the dorsomedial surface of the mandible. Both the anterior and posterior edges of the muscle are slightly convex with the greatest width occurring

medially. There is no indication of a median raphe. This muscle is very uniform in the species examined.

M. intermandibularis posterior (pl. LXX, fig. D).

The *anterior slip* arises on the dorsomedial surface of the mandible and extends fanwise medioventrad between the lateral and medial part of the geniohyoideus lateralis to insert in the ventral aponeurosis. The fibers of the entire muscle are directed caudomediad with the most anterior ones nearly transverse and inserted at the median raphe.

The *posterior slip* arises on the dorsomedial surface of the mandible, beginning less than one millimeter from the posterior tip of the mandible and extending anteriorly for slightly more than one third the length of the mandible. From the origin it extends as a broad fan-shaped muscle and is inserted in the ventral aponeurosis.

M. gularis (pl. LXX, fig. D).

The origin of the gularis is entirely in fascia. The anterior portion (approximately half) arises in a thin aponeurosis which is attached to the quadrate, the squamosal, and the fascia covering the muscles of the otic region. The posterior portion arises from the fascia cephalodorsalis and the skin immediately above it. This muscle is almost completely inserted on the skin of the gular fold, except that a few of the most anterior fibers are inserted in the median raphe. In *complex* and *parvipes* the anterior fibers are just short of the median raphe. In these two species this muscle is also slightly caudad to the tip of the mandible, exposing the insertion of the depressor mandibulae.

M. depressor mandibulae anterior.

The anterior muscle arises from the posterolateral edge of the quadrate, from the squamosal and from the lateral border of the otic capsule. The insertion is on the dorsal half of the posterior tip of the mandible. In all species except *complex*, the fibers arising from the otic capsule lie deep to the cucularis major.

M. depressor mandibulae posterior.

The posterior muscle originates in the fascia cephalodorsalis deep to the gularis but superior to the cucularis major. The insertion is on the ventral surface of the posterior tip of the mandible.

M. quadrato-pectoralis (pl. LXX, fig. D).

The origin of this muscle is mainly on the posterior border and the ventral surface of the squamosal, but the more anterior fibers extend beneath the squamosal and arise from the lateral edge of the otic capsule deep to the dorsal part of the squamosal. This

condition is singular in the genus *Oedipina*. The insertion is in the ventral aponeurosis between the intermandibularis posterior and the gularis. The anterior and posterior fibers may or may not insert deep to the intermandibularis and gularis. In *parvipes* the most posterior fibers insert on the medial part of the gular fold.

M. interhyoideus.

The origin of the interhyoideus is on the anteroventral surface of the ceratohyal, beginning near the distal edge of its dorsal curve and extending for approximately two thirds of the distance to its attachment on the squamosal. It is widely separated from the origin of the quadrato-pectoralis. The insertion of this muscle is in the ventral aponeurosis. However, in *parvipes, complex,* and an undescribed species (number 1419) it is entirely deep to the intermandibularis posterior. In *uniformis* and in a second undescribed species (number 2504) the insertion is deep to the anterior part of the quadrato-pectoralis and to the posterior part of the intermandibularis posterior.

THE LONGITUDINAL AND DEEP MUSCLES

M. geniohyoideus medialis (pl. LXXII, fig. D).

The origin of the muscle is on the posterior surface of the mandible at and immediately lateral to the symphysis. The origin is very narrow, approximately one third the width of the insertion, except in specimen No. 1419 where the lateral fibers lie deep to the median part of the lateralis and provide for a slightly greater width at the origin. In *uniformis* a few of the deep fibers arise from the floor of the mouth a short distance caudad to the fibers originating on the mandible. The insertion is on the ventral surface of the subarcualis rectus 1 and medially along the anterior edge of the inscriptio tendinis. The insertion does not reach the mid-ventral line. The muscle is not straight but curved laterad. The curving is particularly evident along the lateral margin of the muscle, and the insertion is caudad to the posterior tip of the mandible in all species.

M. geniohyoideus lateralis (pl. LXXII, fig. D).

The origin of the lateralis is on the ventral and posterior surface of the mandible lateral to the medialis. The origin is wide, extending laterad from the medialis until it is divided by the intermandibularis anterior and the anterior slip of the intermandibularis posterior. From this point it continues caudad at least to a point level with the center of the eye. In specimen No. 1419 the origin extends to the posterior edge of the eye and is attached along ap-

proximately half of the mandible. The insertion is on the lateral and dorsal surfaces of the ceratohyal, beginning caudad to the posterior tip of the mandible and extending anteriorly approximately to the middle of the cartilage. Those fibers arising mediad to the division extend deep to the lateral fibers and are inserted dorsal to the lateral fibers.

M. rectus cervicis superficialis (pl. LXXII, fig. D).

This muscle arises on the anterolateral margin of the sternal cartilage, and extends anteriorly to the first myocomma where it becomes fused with the profundus. The superficialis does not reach the lateral edge of the profundus at the first myocomma.

M. rectus cervicis profundus (pl. LXXII, fig. D; pl. LXXIV, fig. D).

The major portion of this muscle is a direct continuation of the rectus abdominis but a few of the most medial fibers do arise from the lateral edge of the sternum. The insertion is with the superficialis on the ventromedial surface of the subarcualis rectus 1, and medially along the posterior edge of the inscriptio tendinis to the mid-ventral line. The insertion of the more median fibers is directly ventrad to the first ceratobranchial. This muscle is divided into three segments of nearly equal length. The anterior and posterior segments are nearly equal in length while the middle one is usually slightly shorter than either of the other two. In *parvipes* the posterior segment is noticeably longer. From the medial part of the anterior myocomma deep to the superficial portion of the muscle, a small slip extends anteriorly to insert on the floor of the mouth. The medial fibers of the deep slip are longer than the lateral fibers but do not extend entirely to the suprapeduncularis.

M. subarcualis rectus 1 (pl. LXXII, fig. D; pl. LXXIV, fig. D).

The origin of this muscle is on the ventral, ventrolateral and posterior surfaces of the ceratohyal, beginning in the median part of the ceratohyal at approximately the level of the anterior edge of the suprapeduncularis and extending caudad to the posterior edge of the cartilage, along its posterior margin for a short distance and then across its ventral surface to the lateral border. The lateral part of the muscle extends posterior to the level of the caudal tip of the mandible. The insertion is along the anterior edge of the inscriptio tendinis from the mid-ventral line laterad to the distal ends of the cerato-branchials and caudally along the tendinous sheath surrounding the elongate epibranchial. The fibers of the medial half of the muscle are much shorter in typical *Oedipina* than obtains in other genera studied. The muscle extends beyond

the anterior edge of the front leg in all species seen. It is shortest in *complex* and *parvipes* and longest in *syndactyla* and specimen No. 1419.

A small elongate slip quite apart from the main mass of the muscle arises in a tendinous fascia, which is attached to the ventral surface of the ceratohyal anterior to the suprapeduncularis. The insertion is on the ventral surface of the subarcualis rectus 1 deep to the lateral half of the geniohyoideus medials. The insertion of this muscle is fused with the insertion of the subarcualis rectus 1 and appears to be a specialized slip of this muscle. However, it should be pointed out that except for the insertion the slip is completely separate and distinct from the main muscle, and may represent a new muscle, peculiar to the genus *Oedipina*.

M. suprapeduncularis (pl. LXXIV, fig. D).

The origin of the muscle is on the dorsomedial surface of the ceratohyal, beginning at the base of the attenuated proximal end of the ceratohyal and extending caudad beyond the narrowest space between the two ceratohyals. The muscle is broad for its entire width and the most posterior fibers are the longest. Both conditions are peculiar to the genus *Oedipina*.

M. hyoglossus.

The origin of the hyoglossus is on the anterior tip of the basibranchial between the diagonal cornua. There are no fibers arising from the ventral surface of the anterior tip of the basibranchial as observed in the genus *Chiropterotriton*. The insertion is in a semicircle along the anteroventral surface of the tongue. The fibers are in 6-8 small bundles, rather than in a thin sheet.

VARIATIONS IN THE HYOBRANCHIAL APPARATUS

The anterior ends of the ceratohyals are long and attenuated but are not round and rodlike as in *Thorius*. Medially they are flattened, but lack the medial lobe, which in other genera constricts the posterior part of the suprapeduncularis. Distally they are also attenuated and are curved at more than a ninety degree angle posterior to the tip of the mandible. The ceratohyals are attached to the squamosal by a ligamentous sheath.

SUMMARY

The genus *Oedipina* consists of an uniform assemblage of specialized species. The specializations have not been restricted to one or two muscles but are evident in most of them, particularly in the longitudinal and deep muscles. The ceratohyals have been noticeably modified. These specializations are, however, rather

uniform among the species within the genus and it is quite impossible to refer to any one species as being more generalized than other members of the genus. In no other genus have I encountered such a uniform series of muscular patterns.

GENUS *Lineatriton* Tanner

Lineatriton Tanner, 1950, Great Basin Nat., vol. X, pp. 37-44.

The genus *Lineatriton* as it is now constituted includes only the Mexican terrestrial wormlike salamander *Lineatriton lineola.* This species was formerly included in the genus *Oedipina,* presumably because of its similarity to the species of *Oedipina* in outward appearance and in habitat preference rather than in other characters. Anatomically *L. lineola* has many myological and skeletal (vertebral and hyobranchial) characters that are decidedly different from those found in *Oedipina.*

In spite of the fact that *L. lineola* has reduced the size of its legs, developed a tail as much as twice the length of the head and body, and has taken on a snakelike appearance, it can still be readily distinguished externally from any of the other wormlike salamanders by the reduced number of costal grooves (14) and by the partially free middle digits.

In the following descriptions of the throat musculature and the hyobranchial apparatus other significant anatomical differences between the species *L. lineola* and the species of the genus *Oedipina* will be indicated.

TRANSVERSE THROAT MUSCLES

M. intermandibularis anterior (pl. LXIX, fig. E).

The origin of this muscle is in a small straplike fascia approximately .2 mm medial to the mandible and deep to the anterior edge of the anterior slip of the intermandibularis posterior. The fascia is attached to the mandible and there is no median raphe at the mid-ventral line. Both the anterior and posterior margins are convex and the greatest width, .4 mm., occurs at the mid-ventral line.

M. intermandibularis posterior (pl. LXIX, fig. E).

The *anterior slip* originates on the dorsomedial surface of the mandible approximately 1.3 mm. from the symphysis. The fibers extend fanwise from the origin in a more or less caudomedial direction. Approximately the anterior fifth of the muscle inserts at the median raphe and there is a broad contact posteriorly with the anterior fibers of the posterior slip.

The *posterior slip* originates on the dorsomedial surface of the

posterior third of the mandible. The insertion is in the ventral aponeurosis and extends anteriorly from a line between the posterior tips of the mandibles, to occupy half or more of the distance to the symphysis. The median and posterior fibers extend nearly to the mid-ventral line.

M. gularis (pl. LXIX, fig. E).

The origin of the gularis is in fascia. The anterior part arises in an aponeurosis which is attached to the mandible, quadrate, squamosal and on the muscles and fascia of the otic capsule. The posterior part arises in the fascia cephalodorsalis and from the skin superior to it. The insertion is on the skin of the gular fold and in the ventral fascia along the linea alba. Approximately one third of the insertion is in the ventral fascia (.8 mm.). This is twice the length of the insertion observed in five species of *Oedipina.*

M. depressor mandibulae.

The *anterior muscle* arises on the squamosal and otic capsule, the latter part being deep to the cucularis major. The insertion is on the dorsal half of the posterior tip of the mandible.

The *posterior muscle* originates in the fascia cephalodorsalis deep to the gularis but superior to the cucularis. The insertion is on the ventral half of the posterior tip of the mandible.

Both muscles are distinctly separated from origin to insertion.

M. quadrato-pectoralis (pl. LXIX, fig. E).

The origin of the muscle is mainly on the posterior edge of the squamosal, but a few medial fibers arise from the dorsal tip of the quadrate. There are no fibers extending deep to the squamosal to arise from the ventral surface of the squamosal and the otic capsule as in the genus *Oedipina.* The insertion is in the ventral fascia between the gularis and the intermandibularis posterior. The anterior fibers are inserted deep to the intermandibularis and the posterior fibers reach the linea alba.

M. interhyoideus.

The origin of the interhyoideus is on the anteroventral surface of the ceratohyal beginning at the curve directly caudad to the posterior tip of the mandible and extending craniad at least half way to the attachment of the ceratohyal to the skull. The insertion is in the ventral aponeurosis deep to the posterior part of the intermandibularis posterior. A few fibers insert with the most anterior fibers of the quadrato-pectoralis. The muscle appears to be larger in *L. lineola* than in *Oedipina* of comparable size.

THE LONGITUDINAL AND DEEP MUSCLES

M. geniohyoideus medialis (pl. LXXII, fig. B).

The origin of the medialis is on the posterior surface of the mandible, beginning at the symphysis and extending laterad for approximately .7 mm. There are no fibers arising from the ventral surface of the mandible and the width of the muscle at the origin is nearly twice as wide as in any species of the genus *Oedipina.* The insertion is on the ventral surface of the subarcualis rectus 1, and mediad along the inscriptio tendinis. The muscle at the insertion is only slightly wider than the origin and the medial edge of the insertion is at least half the width of the muscle from the midventral line. The entire insertion is posterior to the caudal tips of the mandibles.

The geniohyoideus medialis is a broad straplike muscle with nearly straight margins for its entire length, not curved or of a variable width as is characteristic of the genus *Oedipina.*

M. geniohyoideus lateralis (pl. LXXII, figs. B & H).

The origin of the lateralis is on the posterior surface of the mandible, mostly lateral to, but with a few medial fibers dorsal to, the medialis. The entire origin lies anterior to the origin of the anterior slip of the intermandibularis posterior and the muscle is completely dorsal to both slips of the intermandibularis. The insertion is on the lateral edge and the dorsal surface of the ceratohyal, beginning at a point just caudad to the posterior tip of the mandible and extending anteriorly to a point near the middle of the ceratohyal.

The geniohyoideus lateralis of *lincola* is simple in structure and has not undergone the specializations existing in *Oedipina.* Actually the origin, insertion, size, shape and general character of this muscle is strikingly similar to that obtaining in the genus *Pseudoeurycea* and is nowise reminiscent of the conditions found in the typical species of *Oedipina.*

M. rectus cervicis superficialis (pl. LXXII, figs. B & H).

The origin of this muscle is on the anterolateral edge of the sternum. From the origin the fibers extend anteriorly along the mid-line and anterolaterad to reach the lateral edge of the profundus at the first myosepta. From this point anteriorly the superficialis and profundus are fused. The insertion is with the profundus. In *Oedipina* the superficialis is proportionately narrower and does not extend to the lateral edge of the profundus.

M. rectus cervicis profundus (pl. LXXII, fig. B).

The lateral and larger part of the profundus muscle is a direct

continuation of the rectus abdominis; while a much smaller medial part arises from the lateral edge of the sternum deep to the superficialis. The muscle inserts laterally on the ventral surface of the subarcualis rectus 1 and medially along the inscriptio tendinis to the mid-ventral line. From the medial part of the anterior myosepta a small slip extends deep to the abdominohyoideus and the second ceratobranchial to insert on the floor of the mouth posterior to the suprapeduncularis and the ceratohyals.

In *lineola* the rectus cervicis is divided into three unequal segments. The middle segment is the shortest and the posterior one is more than twice the combined lengths of the other two. This is quite different from the conditions found in *Oedipina* and is again very similar to the rectus cervicis of *Pseudoeurycea.*

M. rectus cervicis lateralis (as in pl. LXXI, fig. C).

The origin of the lateralis is on the lateral edge of the sternum immediately laterad to the superficialis. The insertion is in fascia on the lateral side of the abdominohyoideus, near the level of the posterior end of the thyroid gland.

M. subarcualis rectus 1 (pl. LXXII, figs. B & H).

The origin of this muscle is on the ventral surface of the ceratohyal, beginning approximately at the level of the anterior edge of the suprapeduncularis where the muscle curves mediad and laterad to the margins of the ceratohyal. The medial part extends caudad along the inner edge for a short distance only, whereas the lateral part extends beyond the posterior tip of the mandible. The insertion extends from the mid-ventral line, laterad along the inscriptio tendinis to the distal ends of the ceratobranchials, and caudally along the tendinous sheath surrounding the epibranchials.

The muscle extends for at least .2 mm. beyond the posterior border of the front leg and is a proportionally longer muscle in *lineola* than in any of the species of the genus *Oedipina.*

M. suprapeduncularis (pl. LXXII, fig. H).

In *lineola* the suprapeduncularis is a small muscle, approximately as wide as it is long and with the fibers noticeably shortened near the posterior border. It lies between the dorsomedial surface of the ceratohyals and extends as a thin transverse muscle across the stalk of the tongue. The origin begins at the base of the anterior spade of the ceratohyal and extends posterior until the ceratohyals approximate each other, by means of the median lobes, at the mid-ventral line. At no point are the fibers more than .5 mm. long.

M. hyoglossus.

The origin is on the anterior edge of the basibranchial between

the base of the cornua. The fibers extend fanwise into the tissue of the tongue anterior to the origin.

VARIATIONS IN THE HYOBRANCHIAL APPARATUS

The proximal ends of each ceratohyal extend anterior as a flattened, lobate, spadelike structure, with the thin medial edges almost in contact at the mid-ventral line. The small suprapeduncularis fits into a concavity between the anterior and the median lobes. The distal ends of the ceratohyals are attenuated, curved at less than a ninety degree angle, and attached to the squamosal by a ligament, as they are in the other genera.

The relative size and shape of the ceratohyals and of the suprapeduncularis muscle in *lineola* is so similar to the same structure in *Pseudoeurycea*, and is completely different from that obtaining in *Oedipina*.

SUMMARY

The species *Lineatriton lineola* is primitive and manifests the more generalized muscle patterns which were presumably present in the ancestral stock of the majority of Mexican salamanders. It is anatomically not closely related to the species of *Oedipina*. This is clearly shown by the entirely different origin of the M. quadratopectoralis, geniohyoideus medialis and geniohyoideus lateralis, and by the distinct variations in the size and shape of the rectus cervicis, the suprapeduncularis and by the equally important diversity in the size and shape of the ceratohyals. The entire anatomical arrangement of the hyobranchial apparatus and its musculature is reminiscent of the general relationship of parts existing in *Pseudoeurycea, Chiropterotriton* and *Parvimolge*. The relationship of *Lineatriton* to *Oedipina* is then, entirely superficial and may best be considered as an excellent example of parallelism in development.

GENUS *Thorius* COPE

Thorius Cope, 1869, Proc. Acad. Nat. Sc. Philadelphia, p. 111. (type *pennatulus*).

The genus *Thorius*, as now restricted, includes seven species of diminutive terrestrial salamanders. Together they form a uniform group decidedly distinct from other Mexican and Central American genera. They are recognized by the presence of an orbitolabial groove, a sublingual fold, a poorly ossified skull, particularly in the dorsal parietal region and by enlarged nostrils. The complete absence of maxillary teeth is also an important characteristic.

The throat muscles are remarkably uniform and show only slight variations in the relative size and shape among the several species. When the throat musculature of *Thorius* is compared with that of other genera the absence of the intermandibularis anterior and the presence of other specializations to be discussed presently, indicates that the genus is as distinct in its myology as it is in external and osteological characters.

THE THROAT MYOLOGY AND THE HYOBRANCHIAL APPARATUS

TRANSVERSE THROAT MUSCLES

M. intermandibularis anterior.

Careful dissection and tissue staining has failed to show any trace of this muscle. I have therefore concluded that it is absent in all species of the genus *Thorius.*

M. intermandibularis posterior (pl. LXVIII, fig. E; pl. LXX, fig. F).

The *anterior slip* originates on the dorsomedial surface of the mandible; the origin is located caudomediad from the symphysis approximately one third to two fifths the length of the mandible. The fibers extend fanwise from the narrow origin and are inserted in the ventral aponeurosis. In *Thorius* there are no fibers inserted along the mid-ventral line. Except for the anterior fibers, which are for the most part transverse, the fiber direction is caudomediad.

The *posterior slip* originates on the dorsomedial surface of the posterior third of the mandible and is inserted in the ventral aponeurosis. This slip is large, fan-shaped, with the anterior fibers extending anteromedially and the posterior fibers extending, slightly caudomedially from the origin to the insertion. No fibers reach the mid-ventral line.

The anterior slip of the intermandibularis posterior in *Thorius* is not enlarged to compensate for the loss of the intermandibularis anterior as it is in the case of *Chiropterotriton abscondens.*

M. gularis (pl. LXX, fig. F).

The origin of the gularis is in fascia, which is attached to the quadrate and squamosal elements, it attaches caudally along the postocular skin-groove and the fascia cephalodorsalis, extending back to, or almost to, the gular fold, except in *minutissimus,* in which it arises entirely from the postocular groove. The anterior half arises in an aponeurosis while the posterior half originates in fascia extending along the skin and the muscles underlying the postocular fold. The insertion is on the skin of the gular fold. The anterior fibers do not reach the mid-ventral line.

In all species this muscle is caudad to the posterior tip of the mandible, thus clearly exposing the insertion of the *M. depressor mandibulae.* In *minutissimus* the depressor mandibulae anterior is entirely exposed.

M. depressor mandibulae anterior (pl. LXX, fig. F).

The anterior muscle arises from the posterolateral edge of the quadrate, the dorsal surface of squamosal and the lateral edge of the otic region of the skull. The dorsal (otic) portion is deep to the cucularis major. The insertion is on the dorsal part of the posterior tip of the mandible.

M. depressor mandibulae posterior (pl. LXX, fig. F).

The posterior muscle arises from the fascia cephalordorsalis deep to the gularis and superior to the cucularis major. The insertion of the posterior muscle is on the ventral part of the posterior tip of the mandible.

M. quadrato-pectoralis (pl. LXX, fig. F).

The origin of the muscle is on the posterior edge of the squamosal with the major portion of it arising from a small posteriorly projecting osseous process. No fibers arise from the quadrate although some appear to arise from the ligament which attaches the ceratohyal to the squamosal. The insertion is in the ventral aponeurosis between the intermandibularis posterior and the gularis.

M. interhyoideus (pl. LXX, fig. F).

The origin of this muscle is on the anteroventral edge of the distal end of the ceratohyal, approximately equidistant between the attachment of this cartilage to the skull, and the point where the ceratohyal is curved caudad to the angle of the jaw. The insertion is in the ventral aponeurosis deep to the posterior slip of the intermandibularis posterior. The interhyoideus is a small narrow muscle and is uniform in the genus *Thorius* except for a wider (.8 mm.) insertion in *troglodytes.*

LONGITUDINAL AND DEEP THROAT MUSCLES

M. geniohyoideus medialis (pl. LXVIII, fig. E; pl. LXXII, fig. C).

The origin of the muscle is on the posterior margin of the mandible beginning at the symphysis and extending laterad for .2 to .5 mm. depending on the size of the specimen. The insertion begins on the ventrolateral surface of the subarcualis rectus 1 and extends medially across the ventral surface of the subarcualis rectus 1 to the lateral edge of the inscriptio tendinis. This muscle is uniform in width for its entire length and is slightly expanded only at its insertion. The insertion is not in a diagonal line but is nearly transverse and is noticeably lateral to the mid-ventral line. This muscle

extends caudad to the posterior tip of the mandible in all species except *pennatulus,* in which it extends only to the level of the posterior tip of the mandible.

M. geniohyoideus lateralis (pl. LXVIII, fig. E; pl. LXXII, fig. C).

The origin of the muscle is on the posterior margin of the mandible lateral to the medialis muscle. There are no fibers arising from the mandible posterior to the anterior slip of the intermandibularis posterior. Some fibers do arise, however, from fascia immediately medial and caudal to the anterior slip. The insertion of this muscle is on the lateral edge and on the dorsal surface of the ceratohyal anterior to the lateral hook of the ceratohyal and extends anteriorly approximately to the middle of this cartilage. Some of the medial fibers extend caudad to the ceratohyal and insert on the floor of the mouth anterior to the deep slip of the rectus cervicis. The insertion extends caudad to the posterior tip of the mandible in all species except *pennatulus* where it is (approximately .2 mm.) anterior to the posterior tip. The belly and insertion are both much wider than the origin.

M. rectus cervicis superficialis (pl. LXXII, fig. C).

The origin of the superficialis is along the anterolateral edge of the sternal cartilage. The origin is narrow, less than half the distance from the mid-line to the lateral edge of the rectus cervicis profundus. The muscle extends anteriorly and anterolaterally to the lateral edge of the profundus at the first myocomma anterior to the sternum. An exception to this is found in *pulmonaris* in which the entire muscle is more narrow and does not reach to the lateral edge of the profundus. The insertion is with the profundus in the inscriptio tendinis.

M. rectus cervicis profundus (pl. LXVIII, fig. E; pl. LXXII, fig. C; pl. LXXIV, figs. A & B).

The major part of this muscle is a direct continuation of the rectus abdominis, however, a few fibers arise on the sternum deep to the lateral edge of the superficialis. The insertion of the lateral part of the muscle is on the ventral surface of the subarcualis rectus 1, while the medial portion inserts along the posterior edge of the inscriptio tendinis. At the anterior myocomma approximately the medial third of the muscle extends deep to the ceratobranchials and the abdominohyoideus to insert on the floor of the mouth. In *pennatulus* the lateral fibers of the deep slip reach the posterior edge of the ceratohyal. There are two myocommata and three unequal segments in this muscle, with the posterior segment approxi-

mately one and a half times as long as either of the other segments.

M. rectus cervicis lateralis.

Careful dissection and staining has failed to reveal any traces of this muscle in the genus *Thorius.*

M. subarcualis rectus 1 (pl. LXXII, fig. C; pl. LXXIV, figs. A & B).

The origin of this muscle is on the ventral surface of the ceratohyal, beginning at the base of the long attenuated anterior end of the ceratohyal, approximately at the anterior edge of the suprapeduncularis, and extending posteriorly along the medial margin of the ceratohyal. The origin of the lateral portion is much longer extending nearly to the posterior tip of the mandible. The medial part of the insertion is along the anterior edge of the inscriptio tendinis; the lateral part is inserted on the posterior ends of the ceratobranchials and along the tendinous sheath surrounding the epibranchial.

In *Thorius* this muscle is short, not extending posterior to the anterior edge of the front leg, except in *macdougalli* where it extends nearly to the posterior border of the leg. The posterior end of this muscle is noticeably rounded and more blunt than it is in other genera. In no other Mexican and Central American genus does this muscle fail to reach caudad to the anterior border of the front leg when the leg is placed at right angles to the body. In some *Chiropterotriton* (*chondrostega, dimidiata* and *chiroptera*) and in *Oedipina complex* and *O. parvipes,* the tip of the muscle reaches approximately to the posterior border of the front leg or slightly beyond. In all other *Chiropterotriton, Oedipina* and other genera here considered, the muscle extends posterior to the leg.

M. suprapeduncularis (pl. LXVIII, fig. E; pl. LXXIV, figs. A & B).

The muscle arises from the dorsomedial edge of the ceratohyal and extends as a thin transverse sheet dorsal to the stalk of the tongue. The fibers of the anterior portion are longest and in the shape of a broad U as they extend caudodorsally across the stalk of the tongue. It is a distinct muscle, quite apart from any other pharyngeal muscle and except in the case of the *pennatulus* it is separated from the deep slip of the rectus cervicis by its width or more. In *pennatulus* it is separated only by approximately half its width.

M. hyoglossus.

The origin is on the anterior tip of the basibranchial between the

cornua. The insertion is in the substance of the tongue anterodorsal to the origin.

VARIATIONS IN THE HYOBRANCHIAL APPARATUS

In all species of *Thorius* the anterior portion of the ceratohyal is extended into a long attenuated rod of cartilage and is in this respect different from all other Mexican and Central American plethodontids.

Hilton (1946:6), in his figures of the hyobranchial skeleton of *Thorius pennatulus*, shows the ceratohyals terminating anteriorly in a broad rounded lobe and the cornua extending at right angles to the basibranchial. In the text of his paper, however, he refers to the hyobranchial apparatus as "slender." I have found the ceratohyals to be greatly attenuated anterior to the suprapeduncularis, and have seen no indication of the ceratohyals becoming expanded and lobate as figured by Hilton (*op. cit.*). I have observed the short cornua extending in an anterolaterad direction from the tips of the basibranchial in all species of the genus. The cornua are certainly not transverse as figured by Hilton.

The most variable part of the apparatus is the size and shape of the ceratohyal. Three types of variation are represented by *pennatulus*, *macdougalli*, and *narisovalis*. (pl. LXVIII, fig. E; pl. LXXIV, figs. A, B & G). The ceratohyal of other species, not figured, are very similar to that of *narisovalis*.

SUMMARY

The genus *Thorius* is unique in that none of its species have retained the intermandibularis anterior or the rectus cervicis lateralis. The extent of myological specialization now present in the species of *Thorius* is indicated by the fact that the loss of these muscles in species of other genera is the exception rather than the rule. The muscle patterns found in the various species of *Thorius* are remarkably uniform and vary only in minor details. Judged by variations in the hyobranchial apparatus and the throat musculature, *pennatulus* is the most variable species of the genus, whereas, *narisovalis* and *minutissimus* are the two most closely related species. Another characteristic feature of the genus *Thorius* worthy of emphasis is the specialization of the anterior part of the ceratohyal into an elongate attenuated rod. Such a modification is not found in the other genera of Mexican and Central American Plethodontidae.

DISCUSSION AND SUMMARY OF THE GENERIC DIFFERENCES AND SIMILARITIES

That there are significant differences existing in the throat anatomy of the Mexican and Central American genera of the family Plethodontidae is evident from the foregoing descriptions.

The genus *Pseudoeurycea* is, as previously stated, apparently the most generalized of the genera under consideration. Its primitiveness is manifested by the broad insertions of the transverse ventral throat muscles, the attachment of the quadrato-pectoralis to the quadrate in the most primitive species, the comparatively large rectus cervicis lateralis, the extremely elongate condition of the subarcualis rectus 1, the broad insertion of the geniohyoideus medialis and the spadelike anterior lobes of the ceratohyal. The origins and insertions of the muscles studied are extensive and there are fewer apparent specializations in the throat myology than in other genera.

The genus *Chiropterotriton* appears to have developed from stock closely related to *Pseudoeurycea*. The origin and insertion of the gularis is only slightly less extensive than in *Pseudoeurycea* and is similar in these genera. The genus *Chiropterotriton* is unique in having the fibers of the hyoglossus arise from the ventral surface of the anterior end of the basiobranchial rather than from the anterior tip. This character is uniform in the genus and does not vary even in the aberrant species *abscondens*. Other variable characters in the genus *Chiropterotriton* are the variation of the origin of the geniohyoideus lateralis, the large size and triangular shape of the intermandibularis anterior and the reduced length of the subarcualis rectus 1.

The anterior lobes of the ceratohyals are similar to those of *Pseudoeurycea* but with this difference; the lateral edge is rather thick and there is a thinning medially giving the appearance of a "blade" rather than that of a spatula or spade.

The genus *Parvimolge* is myologically primitive. Its myology relates it to the genus *Pseudoeurycea*, but is suggestive of a more primitive condition than that of *Chiropterotriton*. *Parvimolge* is similar to *Pseudoeurycea* in several characters; the origin and insertions of the muscles are equally extensive, the intermandibularis anterior is not triangular, the origin of the geniohyoideus muscles is similar and the subarcualis rectus 1 is approximately of the same relative length. The overlapping position of the anterior lobes of

the ceratohyals is unique, but the shape of the lobes resembles more closely that of *Pseudoeurycea* than that of *Chiropterotriton.*

The species *Chiropterotriton dimidiata,* associated with *Parvimolge townsendi* by Dunn (1922:5) and later described as new by Taylor (1940:408), is obviously a *Chiropterotriton.* Its myology is less generalized and the origin of the hyoglossus is typically that of *Chiropterotriton.*

The myology of the salamanders in the genera *Magnadigita* and *Bolitoglossa* is, with the exception of *occidentalis, striatula* and *rufescens,* of a generalized nature and I have been unable to discover a single myological character that would serve to separate all of the species of *Magnadigita* from those of *Bolitoglossa.* The presence of the rectus cervicis lateralis in all but two of the species of *Magnadigita* and its absence in all of the *Bolitoglossa* examined, save *mexicana,* is probably the most reliable character. In general the intermandibularis anterior is relatively shorter and less extensive in *Magnadigita* than in the *Bolitoglossa.*

The genera *Magnadigita* and *Bolitoglossa* have in common the following characters: (1) the suprapeduncularis is noticeably wider than long in most species and (2) there is a large mass of pharyngeal fibers between the suprapeduncularis and the deep slip of the rectus cervicis at least in the less specialized forms. The most significant difference between these two genera and the other genera of the family studied is the shape of the proximal end of the ceratohyal. In other Mexican and Central American genera of plethodontids the proximal end of the ceratohyal is noticeably extended anterior to the suprapeduncularis and is either flattened or attenuated, whereas in *Magnadigita* and *Bolitoglossa* the ceratohyals are not extended, or only slightly so, and terminate in a bluntly rounded end only slightly anterior to the suprapeduncularis muscle. This bluntness of the ceratohyals is, as far as I have been able to discover, the most reliable of the throat characters for the separation of these two genera from other Mexican and Central American plethodontids.

The genus *Oedipina* includes a highly specialized series of species not closely related to any of the other genera studied. Although there are variations in nearly all characters examined, the more significant characters are as follows: The quadrato-pectoralis arises from the posterior edge and the ventral surface of the squamosal, and from the lateral edge of the otic capsule deep to the antero-dorsal edge of the squamosal. Furthermore, the origin of this

muscle is noticeably dorsal to the tip of the quadrate. This condition is unique not only to the Plethodontid salamanders of Mexico and Central America, but also to the remainder of the family Plethodontidae.

A second difference is in the wide and divided origin of the geniohyoideus lateralis. An approach to this condition is found in some *Chiropterotriton* but with this important difference: the fibers arise from the posterior edge of the mandible while in all *Oedipina* the fibers are attached to the ventral surface of the mandible. Furthermore, the medial fibers extend deep to the lateral fibers in *Oedipina* while in *Chiropterotriton* the two parts join and extend caudad as a series of parallel fibers. This I consider a case of homoplassy. The geniohyoideus medialis has an extremely narrow but thicker origin than I have found in other genera. The medialis is always inserted a short distance lateral to the midventral line.

A third difference is found in the division of the rectus cervicis into three nearly equal segments. The posterior segment is approximately equal to the anterior and the middle segment is only slightly shorter than either of the others. This condition is obviously a specialization, since in the generalized genera the posterior segment is as long as the combined lengths of the two other segments.

The genus *Oedipina* is also distinct in having a large suprapeduncularis muscle in which the posterior fibers are as long as or longer than, the anterior or medial fibers. The subarcualis rectus 1 is different from other genera studied in that the muscle has presumably become divided into two heads. A small elongate anterior head and a larger posterior head. The muscle is also noticeably shortened.

The ceratohyals are also distinctive not only in having the proximal end attenuated, but also in lacking the medial lobes which in other genera constrict the posterior portion of the suprapeduncularis.

The species *Lineatriton lineola* is obviously not closely related to the species of the genus *Oedipina*. It does not resemble *Oedipina* in one of the characters listed above and is, as previously stated, myologically more closely related to the genera *Pseudoeurycea* and *Parvimolge* than to any of the other genera studied.

The genus *Thorius* differs noticeably from other Mexican and Central American plethodontids in that all species have lost the intermandibularis anterior and the rectus cervicis lateralis. The subarcualis rectus 1 is shorter than in other Mexican and Central

American genera and the gularis is caudad to the posterior tip of the mandible in all species examined.

The attenuated, rodlike anterior end of the ceratohyal is unique in this genus and although the condition in *Oedipina* approaches that of *Thorius* the shape of the ceratohyals in the two genera is distinctly different and does not serve to relate the two genera.

While there are noticeable myological differences among the various genera of plethodontid salamanders there are also many similarities, particularly in the throat anatomy of the species I consider to be generalized. As previously stated I consider the genus *Pseudoeurycea* to be the most primitive of the Mexican and Central American plethodontids. The generalized conditions of the throat are not only reflected in the myology, but are also evident in the hyobranchial cartilages. A comparison of the throat myology of *Pseudoeurycea bellii* with that found in *Magnadigita robusta* and *Bolitoglossa platydactyla* indicates these species to be very similar, particularly in the following muscles: quadrato-pectoralis, depressor mandibulae, geniohyoideus medialis, geniohyoideus lateralis, interhyoideus, intermandibularis posterior and in the subarcualis rectus 1. Furthermore, the rectus cervicis superficialis reaches the lateral edge of the profundus at the first myocomma anterior to the sternum and the hyoglossus is similar in all three species. Other species in these genera such as *Pseudoeurycea smithi, Magnadigita subpalmata* and *Bolitoglossa flaviventris* are also similar in the general pattern of the throat myology and are only slightly more specialized than the previous species.

Because of these conformities I regard the species *Pseudoeurycea bellii, Magnadigita robusta* and *Bolitoglossa platydactyla* to be representatives of the generalized species in their respective genera.

The establishment of a criterion of generalized species has given a standard for measuring the degree of specialization in other species. One muscle in which specialization is easily followed from the generalized to the specialized species is the quadrato-pectoralis. This muscle arises entirely from the quadrate in *Pseudoeurycea bellii,* and chiefly from the quadrate in *Magnadigita robusta* and *Bolitoglossa platydactyla,* but with a few fibers arising from the squamosal in the last two species. In several species of each genus the quadrato-pectoralis arises almost equally from the quadrate and squamosal. In the specialized species of *Pseudoeurycea cochranae, Magnadigita dunni* and *Bolitoglossa rufescens* the origin of this muscle has shifted dorsally and arises only from the squamosal. In the other genera of Mexican and Central American plethodontids this muscle originates principally or entirely on the

squamosal. Thus there appears to be an orthogenetic type of development for the origin of this muscle.

The subarcualis rectus 1 is relatively longest in the primitive species of the Mexican and Central American plethodontids and shortest in the specialized species of *Oedipina* and *Thorius*. In *Hydromantes* this muscle is comparable to that found in the most generalized of the Mexican and Central American species.

The rectus cervicis is similar in the generalized species. In such species the muscle is divided into three unequal segments the posterior of which is as long as the combined lengths of the other two and the superficialis muscle reaches the lateral edge of the profundus at the first myocomma anterior to the sternum. In the more specialized species of *Pseudoeurycea, Magnadigita, Bolitoglossa* and in particular, all species of *Oedipina,* the segments are nearly equal in length and the superficialis does not reach the lateral edge of the profundus.

The median and distal parts of the ceratohyal are very similar throughout all the genera except *Oedipina.* There are variations in the size of the medial lobe and in the angle of the distal hook but otherwise the ceratohyals are essentially the same. The proximal end of the ceratohyal has been variously modified in all genera of Mexican and Central American plethodontids. The primitive condition was presumably spatulate or at least with an enlarged lobe of thin cartilage. I consider the proximal part of the ceratohyals of *Pseudoeurycea, Parvimolge,* and *Lineatrition* to be most similar to the presumed ancestral condition, *Chiropterotriton* is only slightly modified from the ancestral type. The major specializations have taken place in two directions, toward a loss of the proximal lobe in *Magnadigita* and *Bolitoglossa* and toward an attenuation in *Oedipina* and *Thorius.*

I have previously spoken of the broad insertion of the transverse muscles as indicative of primitiveness in *Pseudoeurycea.* In *Magnadigita* and *Bolitoglossa* the insertions of these muscles in the generalized species are also broad, but less so than in *Pseudoeurycea.* There is also a similarity in that the gularis covers the posterior tip of the mandible in the generalized species of all three genera. The intermandibularis anterior has, as in the case of the proximal end of the ceratohyal and in contrast to the quadratopectoralis, become variously modified in the genera of the Mexican and Central American plethodontids. In *Pseudoeurycea* there is an indication that the intermandibularis is being reduced, or even lost in some species, while in others the muscle is large and is becoming much enlarged medially, as in some *Chiropterotriton.* In

the species of *Bolitoglossa* and *Magnadigita* I have found the intermandibularis anterior to be a relatively small muscle when compared with *Pseudoeurycea gigantea* and an even smaller muscle when compared with *Pseudoeurycea leprosa* or with any of the species of *Chiropterotriton*. In the species of *Chiropterotriton* the anterior muscle is large, reaching its highest development as a triangular shaped muscle in *terrestris* and *multidentata*. In *Parvimolge* this muscle is well developed, but does not reach the relative size of that in some *Chiropterotriton*. In *Magnadigita* the muscle has become shortened and narrowed. This is also true for *Bolitoglossa flaviventris*. In *Bolitoglossa striatula* and *Bolitoglossa rufescens* the muscle has become much elongated and is narrow medially. The relative size and shape of the intermandibularis anterior was undoubtedly present in the ancestral stock of these salamanders. Two divergent evolutionary trends are obvious, either a reduction in size leading to its final loss or to an enlargement.

In spite of the obvious difference in the ceratohyals of the various genera and in the modification of the intermandibularis anterior, the rectus cervicis lateralis and the suprapeduncularis, the generalized species are very similar myologically and represent the primitive conditions which existed in the primitive stock of the Mexican and Central American Plethodontidae. These data have led me to conclude that these genera arose from similar ancestral stock, whose characteristics were: that the quadrato-pectoralis was originally attached only to the quadrate; that the intermandibularis was present in the ancestral stock; that the subarcualis rectus 1 was greatly elongated and specialized; that the proximal end of the ceratohyal was originally spatulate; that the rectus cervicis was divided into three unequal segments, the posterior of which was approximately as long as the combined lengths of the other segments; and that the rectus cervicis lateralis was well formed.

By utilizing both the differences and conformities that exist or are extant, it is possible to arrange the Mexican and Central American genera into the following series of related groups:

Group I	Group II
Pseudoeurycea	*Magnadigita*
Chiropterotriton	*Bolitoglossa*
Parvimolge	
Lineatriton	
Group III	Group IV
Oedipina	*Thorius*

The fact that some genera are grouped together does not invalidate their distinctness as genera. The groups are a means of showing what I have concluded to be the lines of descent among the Mexican and Central American salamanders.

PHYLOGENETIC CONSIDERATIONS

Besides fulfilling the purpose of this investigation, the study has added materially to our understanding of the throat anatomy of the Plethodontidae, and has provided a much broader picture, not only of the Mexican and Central American forms, but also of the entire family.

This study has confirmed many opinions concerning the phylogenetic position of the salamanders of these genera. It has, however, shown that some opinions must be discarded or viewed with considerable doubt. Though there are varying opinions regarding the taxonomy of these salamanders, I am convinced that at least eight, and possibly nine, genera must be recognized. These conform to those listed by Taylor (1944), and are characterized not only by the characters used by Taylor (*op. cit.*) but also by the characteristics of the throat anatomy brought to light by this investigation. It is not impossible that further generic separation will be necessary when the Mexican and Central American Plethodontidae are more completely known.

The Mexican and Central American Plethodontidae here considered are similar in that all have a free tongue, a character I consider to have been established in the ancestral stock before its migration into Mexico. The primitive characteristics of the genus *Gyrinophilus* of eastern United States as indicated by Dunn (1926:27) and Piatt (1935:227) suggest that the ancestral free-tongued species had a very early origin. There is no way of knowing exactly when such a character arose; however, if we accept the Pliocene as stated by Dunn (1926:32) as a possible time of migration, then it is seemingly safe to assume the Miocene as a possible time for its development. The character must have been extant sometime before the invasion of Mexico by the plethodontid salamanders. Furthermore, there is in the free-tongued species a great diversity of other characters in the genera, from the primitive genus *Gyrinophilus*, having many salamandridlike characters, to the highly specialized species of the genera *Oedipina* and *Thorius*. I am convinced that the data thus far gathered by other workers and those resulting from these investigation indicate

a very early beginning for the free-tongued condition in the Plethodontidae.

I can find no valid reason for accepting two separate origins for the character of a free tongue in these salamanders. Piatt (1935: 235) has suggested that the genera of his *Gyrinophilus* group had an origin quite apart from the genus *Hydromantes* and likewise from the genera of Mexico and Central America. The idea of a separate origin is based primarily on the presence of the lingual cartilage in the *Gyrinophilus* group, a character thought to be homologous to the "sehnenplatte" of the Salamandridae. Though the lingual cartilage may serve directly to relate the *Gyrinophilus* group to the primitive conditions found in *Salamandra,* it does not suggest (to me at least) an origin for this group separate from that of other free-tongued Plethodontids. The *Gyrinophilus* group and part of the Mexican and Central American genera (*Pseudoeurycea, Parvimolge, Chiropterotriton, Oedipina, Lineatriton,* and *Thorius*) are all characterized by the presence of a sublingual fold. This fold is attached to the floor of the mouth in almost the same position as the tissue used to attach the tongue in such genera as *Plethodon* and may represent a retention of this tissue in the free-tongued forms. In other words, the sublingual fold relates the two major groups which Piatt would derive separately on the basis of a lingual cartilage. Furthermore, *Gyrinophilus* and *Hydromantes,* two quite different genera, are similar, as well as primitive, in that both possess double premaxillae. I am not contending that the two genera listed are closely related, but the character of double premaxillae does indicate that they may have stemmed from a similar ancestry. The hyobranchial apparatus and its musculature are similar and, as suggested by Piatt (1935:234), "give morphological evidence of community of descent at a very early date."

The presence of the lingual cartilage in *Gyrinophilus* definitely indicates a primitive condition referable to a direct descent from the ancestral plethodontid stock. Its absence does not, however, mean that the cartilage could not have been lost in certain groups after the development of the free-tongued condition. Piatt (1935:236), in attempting to relate *Batrachoseps* to *Hydromantes* and *Oedipus,* states, "The os thyreoideum in *Batrachoseps* is much more reduced than in *Gyrinophilus* and could, I think, be explained as a foreshadowing of the conditions in *Hydromantes* and *Oedipus.*" If it be possible to postulate close relationship between genera having a second basibranchial to those without such a bone, then

it is just as reasonable to postulate relationships between groups with a lingual cartilage to those without such a cartilage. I am not attempting to suggest a close relationship but rather to emphasize an early relationship among the free-tongued plethodontid salamanders.

The ancestral stock gave rise, then, to two diverging groups of genera. One of these is the *Gyrinophilus* group, including *Gyrinophilus,* the one most nearly approximating the ancestral stock of the line and including *Pseudotriton, Eurycea,* and *Manculus.* The other line includes all other genera of free-tongued salamanders, all of which have arisen from an ancestral stock presumably similar to that of *Gyrinophilus,* but which have, because of migration, isolation, adaptation, and possibly other causes, become highly modified from the ancestral stock. In the second group the os thyreoideum and the omohyoideus have been lost, and the intermandibularis anterior has been retained. The ceratohyals have been modified anteriorly, the first ceratobranchial is smaller than the second, and there has been a noticeable enlargement in the size of the quadrato-pectoralis. A further specialization is apparent in the development of enlarged subdigital pads under the distal phlanges, or in the webbing between the toes, or in both.

The ancestral stock of the Mexican and Central American plethodontids appears to have been divided early into two of the present day lines. The one line is distinct from the other in the retention of a distinct sublingual fold (Taylor 1944:203), a primitive characteristic and one which relates the group more directly to the main line of descent. This branch includes the genera *Pseudoeurycea, Parvimolge, Chiropterotriton, Oedipina, Lineatriton,* and *Thorius.*

The other line includes *Bolitoglossa, Magnadigita,* and possibly *Hydromantes,* although the last genus is primitive and has unquestionably been separated from the other two genera for a greater length of time. These genera are similar in that all have lost the sublingual fold, and the first ceratobranchial is smaller than the second. The myology of *Hydromantes* is more nearly similar to that of some *Magnadigita* or *Bolitoglossa* than to that of other Mexican and Central American species. In *Hydromantes* the omohyoideus and rectus cervicis lateralis are both absent, the suprapeduncularis is similar to that of *Bolitoglossa platydactyla,* and the subarcualis rectus 1 is also very similar in length and origin. The depressor mandibulae is distinctly divided into two muscles

and has a similar origin and insertion in all. There are commonly thirteen costal grooves in all three genera.

There are, however, many fundamental differences between *Hydromantes* and the other two genera. In *Hydromantes* there are two premaxillae; the paravomerine teeth are separated from each other by a distinct space; the first basibranchial is flattened medially and proximally and is devoid of cornua; the ceratohyal is attached to the dorsal tip of the quadrate rather than to the squamosal; the quadrato-pectoralis arises entirely from the distal end of the ceratohyal and is closely associated with the interhyoideus; the intermandibularis anterior is absent; the gularis, though distinct and similar in origin and insertion, is noticeably smaller, and the tail is not constricted at its base. This list of characteristics clearly indicates the primitive condition of *Hydromantes,* and although its relationships are with *Magnadigita* and *Bolitoglossa,* there is good reason to believe that the genus *Hydromantes* became isolated from the parental stock of the *Bolitoglossa* line soon after its origin.

As previously indicated, the genera *Magnadigita* and *Bolitoglossa* are closely related. The throat anatomy is generalized and similar, varying so slightly that no single character will serve to separate them. In both genera the ceratohyals are similarly modified, the vertebrae are amphicoelous, and both have prefrontal bones. They are different in that the feet of the *Bolitoglossa* are fully webbed or have at most only the sharp extreme tips of the fingers and toes free. The palms and soles are smooth, and the subdigital pads are lacking under the distal phalanges. In the genus *Magnadigita* the digits of hand and foot are widely spread; the proximal phalanges are included in a heavy webbing; The distal phalanges are free, truncate, and have the subdigital pads well developed. The two middle digits are relatively shortened, giving the appearance of a shorter, more stubby hand or foot than is found in other genera.

The feet of both *Magnadigita* and *Bolitoglossa* are adapted for an arboreal type of life, although there are one or more species in each of the two genera which are presumably terrestrial. The species of the genus *Bolitoglossa* are more specialized in foot type than are the species of *Magnadigita.* In smaller species of *Bolitoglossa,* such as *occidentalis* and *rufescens,* the tail is much shorter than the combined lengths of head and body, the costal grooves are entirely obliterated in most specimens, and the digits are inclosed in a very heavy padlike webbing. The myology of the throat is strikingly different from that of most *Bolitoglossa,* and the first epibranchial is slightly reduced in length. The species *Bolitoglossa*

rufescens is more closely related to *occidentalis* than to other *Bolitoglossa*. These two species differ chiefly in that the maxilla is toothless in *rufescens* and toothed in *occidentalis* (Taylor 1941: 145): otherwise they are similar. They are certainly the most specialized and divergent species of the genus, and it is questionable whether one should include these species in the genus *Bolitoglossa*.

The other large branch of the Mexican and Central American plethodontids, (*Pseudoeurycea, Parvimolge, Chiropterotriton, Lineatriton, Oedipina,* and *Thorius*) became divided into three divergent evolutionary lines, designated hereafter as the *Thorius* line, *Oedipina* line and the *Pseudoeurycea* line.

The phylogenetic position of the genus *Thorius* is less certain than that of any of the other Mexican and Central American genera, chiefly because it is the most divergent and specialized of the genera. Since its description and its elevation to family rank by Cope (1869), the genus has been subject to more taxonomic changes than any of the genera described for that region. This in itself is indicative of the uncertainty on the part of previous workers of the actual status of the *Thorius* line. Taylor (1944:192-197) has given a rather detailed history of the genus to that date. Since then Smith and Taylor (1948:16) have placed the genus *Thorius* in the subfamily Thoriinae. This later arrangement is based not only on the marked divergences in the external, dental, and skull characters, but also on the opisthocoelous type of vertebral articulation found in the genus. There is, however, no doubt concerning the distinctiveness of the genus from all other free-tongued plethodontids, and I am convinced that the species of this genus are not, as suggested by Dunn (1926:33), closely related to *Parvimolge townsendi* or *Chiropterotriton nasalis*. I have not seen *Chiropterotriton picadoi* and can offer no opinion on its relationship.

The genus *Thorius* differs strikingly from all the plethodontid salamanders of Central America and Mexico. The following characters are unique in this genus: an orbitolabial groove not intercepted by a notch; edentate maxillae in all species; the invariable absence of both the intermandibularis anterior and the rectus cervicis lateralis; a small posterior lobe for the attachment of the quadrato-pectoralis present on the squamosal; the proximal end of the ceratohyal attentuated and rodlike; the dorsum of the skull not ossified; and the vertebrae opisthocoelous rather than amphicoelous. In the light of all these differences, the myological similarities between *Thorius* and such genera as *Pseudoeurycea, Parvimolge*

and *Chiropterotriton* seem susceptible to interpretation as a case of convergence, although the myological similarities and the presence of the sublingual fold might, on equally logical grounds, be assumed to reflect genetic homogeny. In spite of all previous studies and new information discovered in the course of my investigation, the phylogenetic position of the genus *Thorius* cannot now be firmly established.

The genus *Manculus* of the Eastern United States has an orbitolabial groove but with this difference: the groove is intercepted by a notch in the lip which extends dorsad near the posterior edge of the eye. In *Thorius* the groove is not intercepted by a notch, but enters the mouth directly. A foreshadowing of the conditions found in *Manculus* is present in *Eurycea*, in which the notch is present but does not completely intercept the groove.

In the genus *Batrachoseps* the median part of the brain case is also membranous, but I do not consider that this character relates the genus *Batrachoseps* to the genus *Thorius*. The two genera are otherwise substantially different, and it appears that the poorly ossified skull is an example of fortuitous convergence. Both genera are terrestrial and subterrestrial in habits and might in this respect have been affected similarly by the environment. In the genus *Batrachoseps* the myology is noticeably different from that of all other genera studied, and I consider its association with *Hydromantes* and the Mexican and Central American plethodontids as suggested by Piatt (1935:232) to be entirely unwarranted. The genus *Batrachoseps* is itself a highly specialized tongue-tied group of salamanders. Its relationships are presumably with the genus *Plethodon* rather than with any of the free-tongued groups.

The relationships of the genus *Oedipina* are seemingly also with those of the Mexican and Central American genera having a sublingual fold. Most of the throat muscles of this genus are more specialized than those of *Thorius*, and moreover *Oedipina* appears to be equally specialized regarding the hyobranchial apparatus. The two genera have undergone specialization in different ways and are widely separated, even though there may be a few rather noticeable similarities in the throat myology of the two genera.

Hilton (1947:38) described the genus *Oedopinola* and designated the Panamanian species *Oedipina complex* (Dunn) as the type species and also included *Oedipina parvipes* (Peters) in the genus. The generic characters presented by Hilton (1946:38) are as follows: "Short snout. Hands and feet without free toes. Single premaxillary with a single long cylindrical shaft before forking

caudally. Slight fontanelle. Vertebrae not long, no alar folds. Nineteen vertebrae before the sacral. Carpus and tarsus with a few larger cartilages but mostly smaller." I have dissected both Panamanian species and have found them to be very similar to *Oedipina uniformis* Keferstein in their throat anatomy (Tanner 1950:37). Unfortunately Hilton's comparisons appear to have been made with the species *Lineatriton lineola* and not with any of the species in the genus *Oedipina*. This fact obviously accounts for the many differences observed by Hilton. It is therefore necessary to retain the species *complex* and *parvipes* in the genus *Oedipina* and to place the genus *Oedopinola* Hilton as a synonym under the genus *Oedipina* Keferstein.

The genus *Pseudoeurycea* is the most primitive of the Mexican and Central American plethodontids and as such forms the main stem for the remainder of the genera. The primitive characteristics are reflected not only in the hyobranchial apparatus and its musculature, but also in the entirely free digits of the hands and feet. In the species *P. cephalica* there is a partial webbing of the proximal digits, a condition not found, so far as I am aware, in other species of the genus. Despite the fact that the foot is slightly webbed, the hyobranchial apparatus and the myology of *cephalica*, together with other significant characteristics, are very similar to other *Pseudoeurycea*, and point to no close relationship with other genera.

The genus *Chiropterotriton* appears to have been derived from the genus *Pseudoeurycea*. The origin of the genus has not been recent, however, inasmuch as the genus *Chiropterotriton* has undergone adaptive radiation and its species are specialized. The genus is most similar to the species of group III of *Pseudoeurycea*, and I suspect its origin to be with this group. The two genera differ as follows: the proximal ends of the ceratohyals have been modified; the hyoglossus has become attached to the ventral surface of the basibranchial; the subarcualis rectus 1 has become relatively shorter; and the intermandibularis anterior is present and relatively larger than in most *Pseudoeurycea*. The digits are widely spread, and the proximal phalanges of the hands and feet are enclosed in a webbing.

The throat myology and the hyobranchial apparatus of the genus *Parvimolge* relates it to the *Pseudoeurycea* line. The muscle patterns are more in accordance with those of *Pseudoeurycea* than they are with *Chiropterotriton*. The ceratohyals and the relatively elongate epibranchials are very similar to *Pseudoeurycea*.

However, in the genus *Parvimolge* the fingers and toes are more completely webbed than are those of *Chiropterotriton* and lie close together rather than widely spread as in the latter genus. The middle finger and the middle toe are noticeably longer and are pointed rather than rounded. The foot type is more nearly like that of *Lineatriton* than any other type seen in the Mexican and Central American species.

Dunn (1926) suggested that the species *Parvimolge townsendi* is an annectant form relating *Thorius pennatulus* to the species now considered as belonging to the genus *Chiropterotriton.* I have been unable to find any characters in the throat anatomy that would relate *Parvimolge* directly to either of the above genera or to any other genus of free-tongued Mexican or Central American plethodontids.

The species *Lineatriton lineola* is so similar in its throat anatomy to the genera *Pseudoeurycea, Chiropterotriton* and *Parvimolge* and so different from the genus *Oedipina* that I have found it advisable to associate the genus *Lineatriton* with the *Pseudoeurycea* evolutionary line. A careful comparison of the figures of *L. lineola* (pl. LXIX, fig. E; pl. LXXII, fig. B) with the figures of *O. uniformis* (pl. LXX, fig. D; pl. LXXII, fig. D) will indicate the distinct differences between these two genera. If the figures of *L. lineola* are now compared to the figures of *Pseudoeurycea,* the similarity of *L. lineola* to the species of the genus *Pseudoeurycea* is as obvious as are its differences from *O. uniformis.* Furthermore, the feet of *L. lineola* are not typical of the genus *Oedipina,* but are less webbed and may be compared more favorably with those found in the genus *Parvimolge.*

In view of the differences between the species *L. lineola* and the species of *Oedipina* as regards the throat myology, the hyobranchial apparatus, the hands and feet, the vertebrae, and other significant characters, and the obvious similarities of *L. lineola* to the species of *Pseudoeurycea* line, I cannot regard this species as a member of the genus *Oedipina.* Further anatomical study (Tanner 1950) has pointed to the necessity of describing the new genus *Lineatriton* to receive this species.

The following diagram (Fig. 5) illustrates the opinion herein expressed concerning the phylogeny of the free-tongued Plethodontidae. Although the diagram is based primarily on the throat anatomy, other characters have also been used in arriving at the relationships.

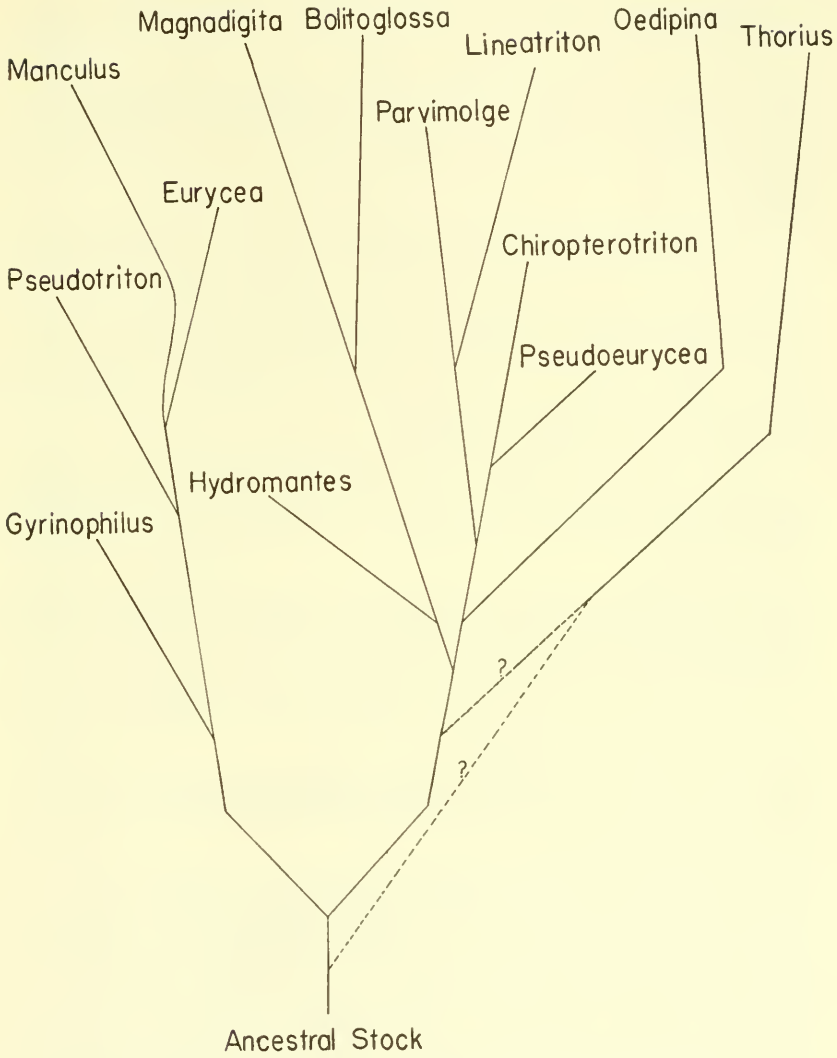

FIG. 5. Phylogeny of the free-tongued Plethodontidae.

SUMMARY AND CONCLUSIONS

1. The intermandibularis anterior is present in most species and in all genera of Mexican and Central American plethodontids, except *Thorius*.

2. The origin of the quadrato-pectoralis is variable among the species and among the genera. In those species here considered

as generalized, the origin is on the quadrate, whereas in specialized species the muscle arises from the squamosal.

3. The gularis has an extensive origin and an extensive insertion in the generalized species. In specialized species the anterior edge of the muscle is posterior to the caudal tip of the mandible, and the number of fibers inserted in the ventral aponeurosis is greatly reduced.

4. The interhyoideus is rotated at 180 degrees from the origin to the insertion and is distinct from the quadrato-pectoralis in all genera of Mexican and Central American Plethodontidae.

5. The depressor mandibulae is divided into two separate muscles in all genera of Mexican and Central American Plethodontidae and is herein considered as the depressor mandibulae anterior and the depressor mandibulae posterior.

6. The origin of the geniohyoideus lateralis is more variable than that of the geniohyoideus medialis. It is particularly variable in the arboreal species of the genus *Chiropterotriton* and in the genus *Oedipina*.

7. The rectus cervicis is divisible into three unequal segments. In the generalized species the posterior segment is as long as the combined length of the two anterior segments.

8. There is a small medial slip extending deep from the anterior myocomma of the rectus cervicis, which I have designated as the deep slip of the rectus cervicis.

9. A small, narrow muscle, presumably derived from the lateral edge of the rectus cervicis, is described as new and designated the rectus vervicis lateralis.

10. The omohyoideus muscle is not present in the Mexican and Central American genera of free-tongued Plethodontidae.

11. The subarcualis rectus I is highly specialized in all genera studied, but is proportionally longer in the generalized species. In *Oedipina* this muscle has been divided into two heads.

12. The suprapeduncularis is distinctly separated from all pharyngeal fibers and from the deep slip of the rectus cervicis. It is characterized by having the anterior margin indented, giving the appearance of a broad U.

13. In all *Chiropterotriton* the hyoglossus originates on the ventral surface of the anterior tip of the basibranchial. This is considered to be a unique specialization.

14. The second basibranchial (os thyreoideum) is absent in all genera of Mexican and Central American plethodontids. In its place is a connective tissue vestige known as the inscriptio tendinis.

15. The proximal end of the ceratohyal is sufficiently modified in the Mexican and Central American plethodontids to be used as a character in the separation of the genera.

16. There is sufficient evidence in the throat anatomy of the Mexican and Central American genera of plethodontid salamanders to provide a basis for separating them into at least eight genera.

17. It is postulated that the free-tongued condition is homologous among plethodontid salamanders, and that the ancestors of the Mexican and Central American genera were free-tongued before migration to Mexico.

18. On the basis of the throat anatomy the genus *Pseudoeurycea* is the most primitive, whereas the genera *Oedipina* and *Thorius* are the most specialized of all the genera.

19. The species *Lineatriton lineola* has been associated with the generalized genera *Pseudoeurycea* and *Parvimolge*.

20. The species *Chiropterotriton abscondens* and *Bolitiglossa rufescens* are atypical, and represent the extremes of variation within these genera.

21. On the basis of the throat anatomy and other concomitant data, the genera of Mexican and Central American Plethodontidae here recognized are believed to have arisen from similar primitive stock through four separate lines of descent.

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KEY TO ABBREVIATIONS USED ON PLATES

SKELETON

Bb1, first basibranchial.
Cb1, first ceratobranchial.
Cb2, second ceratobranchial.
Ch, ceratohyal.
Cor, cornu.
Eb1, first epibranchial.
Md, mandible.
Sc, sternum.

MUSCLES

Ah, abdominohyoideus.
Chi, subarcualis rectus 1.
Drc, deep slip of rectus cervicis.
Ghl, geniohyoideus lateralis.
Ghm, geniohyoideus medialis.
Hg, hyoglossus.
Ih, (fig. B) interhyoideus.
Ih, (fig. D) quadrato-pectoralis.
Ina, intermandibularis anterior.
Inpa, intermandibularis posterior anterior slip.
Inp, intermandibularis posterior.
Qp, (fig. D) interhyoideus.
Ra, rectus abdominis.
Rc, rectus cervicis profundus.
Rcs, rectus cervicis superficialis.
Sp, suprapeduncularis.

PLATE LXVIII

FIG. A. *Chiropterotriton arborea* (Taylor). Transverse and longitudinal ventral throat muscles. E. H. T. No. 16748. × 5.

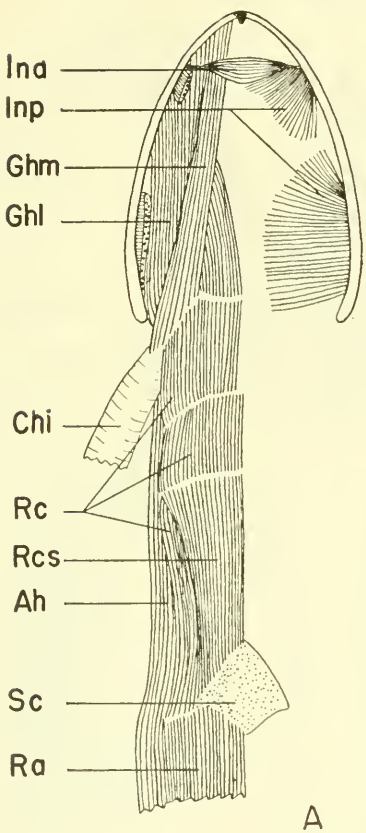
FIG. B. *Chiropterotriton arborea* (Taylor). The deep throat muscles and the ceratohyals. E. H. T. No. 16748. × 5.

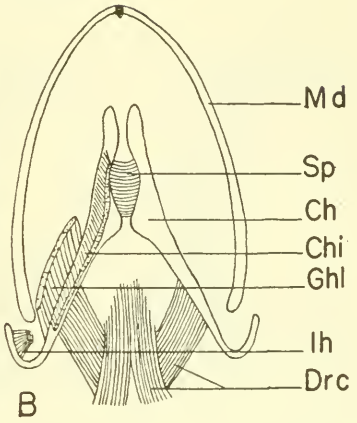
FIG. C. *Chiropterotriton multidentata* (Taylor). The branchial cartilages and the M. hyoglossus. E. H. T. No. 25481. × 6.

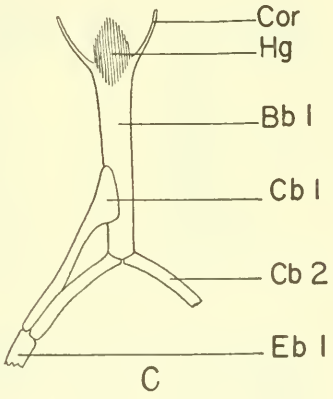
FIG. D. *Pseudoeurycea rex* (Dunn). Transverse ventral throat muscles. E. H. T. No. 27281. × 5.

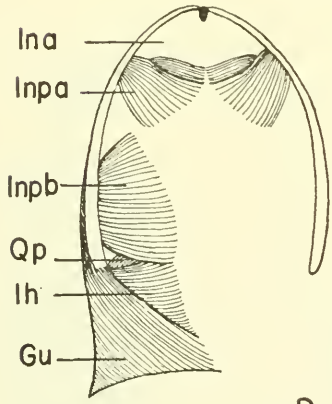
FIG. E. *Thorius pennatulus* (Cope). The deep throat muscles and the ceratohyals. E. H. T. No. 25227. × 10.

PLATE LXVIII









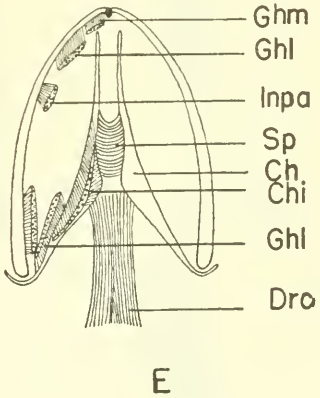


PLATE LXIX

FIG. A. *Chiropterotriton multidentata* (Taylor). Transverse ventral throat muscles. E. H. T. No. 25481. × 6.

FIG. B. *Pseudoeurycea gigantea* (Taylor). Transverse ventral throat muscles. E. H. T. No. 28910. × 2½.

FIG. C. *Pseudoeurycea goebeli* (Schmidt). Transverse ventral throat muscles. E. H. T. No. 20301. × 4.

FIG. D. *Chiropterotriton terrestris* (Taylor). Transverse ventral throat muscles. E. H. T. No. 23309. × 10.

FIG. E. *Lineatriton lineola* (Cope). Transverse ventral throat muscles. E. H. T. No. 26583. × 7½.

FIG. F. *Parvimolge townsendi* (Dunn). Transverse ventral throat muscles. E. H. T. No. 31572. × 10.

FIG. G. *Chiropterotriton chondrostega* (Taylor). Transverse ventral throat muscles. E. H. T. No. 17297. × 7½.

FIG. H. *Chiropterotriton chiroptera* (Cope). Transverse ventral throat muscles. E. H. T. No. 29315. × 5.

FIG. I. *Pseudoeurycea nigromaculata* (Taylor). Transverse ventral throat muscles. E. H. T. No. 24603. × 5.

FIG. J. *Chiropterotriton xolocalcae* (Taylor). Transverse ventral throat muscles. E. H. T. No. 25313. × 5.

FIG. K. *Chiropterotriton abscondens* Taylor. Transverse ventral throat muscles. E. H. T. No. 1410. × 7½.

PLATE LXIX

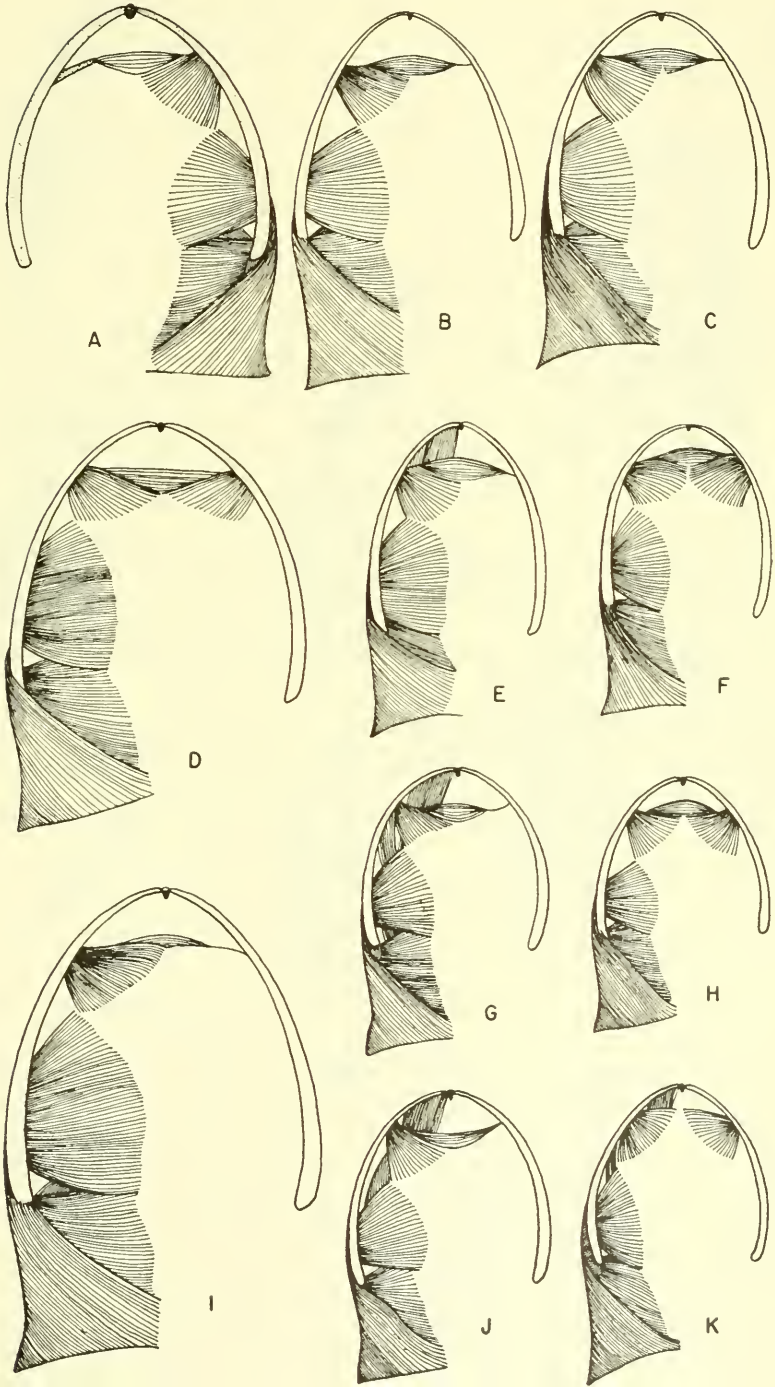


PLATE LXX

FIG. A. *Batrachoseps a. attenuatus* (Eschscholtz). Transverse ventral throat muscles. Univ. of Kans. Mus. Nat. Hist. No. 5098. × 7½.

FIG. B. *Magnadigita robusta* (Cope). Transverse ventral throat muscles. E. H. T. No. 25074. × 3.

FIG. C. *Magnadigita nigroflavescens* (Taylor). Transverse ventral throat muscles. E. H. T. No. 26784. × 5.

FIG. D. *Oedipina uniformis* Keferstein. Transverse ventral throat muscles. E. H. T. No. 1021. × 5.

FIG. E. *Parvimolge townsendi* (Dunn). The deep throat muscles and the ceratohyals. E. H. T. No. 31572. × 7½.

FIG. F. *Thorius narisovalis* Taylor. Transverse ventral throat muscles. E. H. T. No. 25041. × 10.

FIG. G. *Bolitoglossa rufescens* (Cope). Transverse ventral throat muscles. E. H. T. No. 18863. × 7½.

FIG. H. *Bolitoglossa flaviventris* (Schmidt). Transverse ventral throat muscles. E. H. T. No. S17076. × 3.

FIG. I. *Bolitoglossa striatula* (Noble). Transverse ventral throat muscles. E. H. T. No. 402. × 4.

FIG. J. *Bolitoglossa occidentalis* Taylor. Transverse ventral throat muscles. E. H. T. No. 28121. × 5.

PLATE LXX

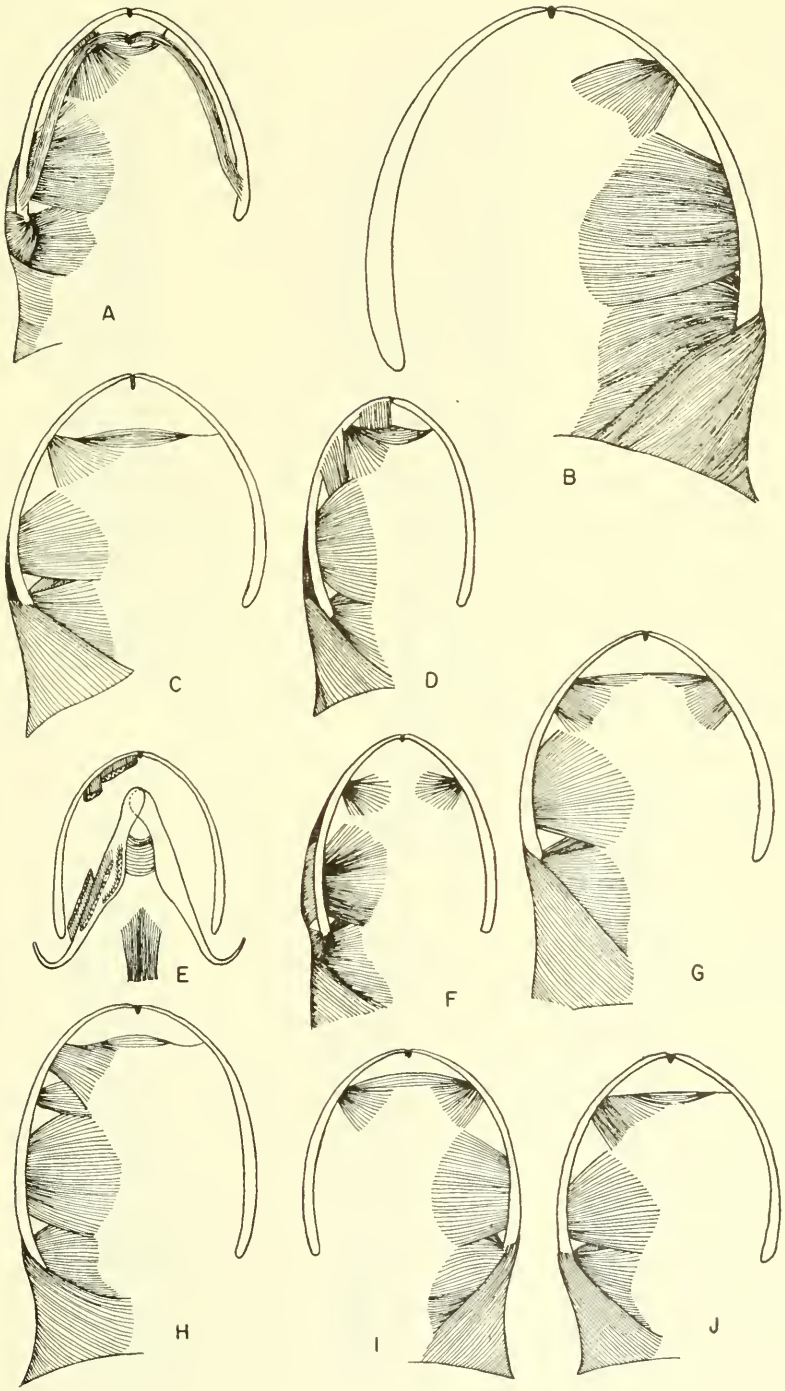


PLATE LXXI

FIG. A. *Pseudoeurycea nigromaculata* (Taylor). Longitudinal throat muscles. E. H. T. No. 24603. × 5.

FIG. B. *Bolitoglossa platydactyla* (Cuvier). Longitudinal throat muscles. E. H. T. No. 16321. × 5.

FIG. C. *Pseudoeurycea gigantea* (Taylor). Longitudinal throat muscles. E. H. T. No. 28910. × 2½.

FIG. D. *Chiropterotriton chiroptera* (Cope). Longitudinal throat muscles. E. H. T. No. 29315. × 5.

FIG. E. *Pseudoeurycea goebeli* (Schmidt). Longitudinal throat muscles. E. H. T. No. 20301. × 4.

PLATE LXXI

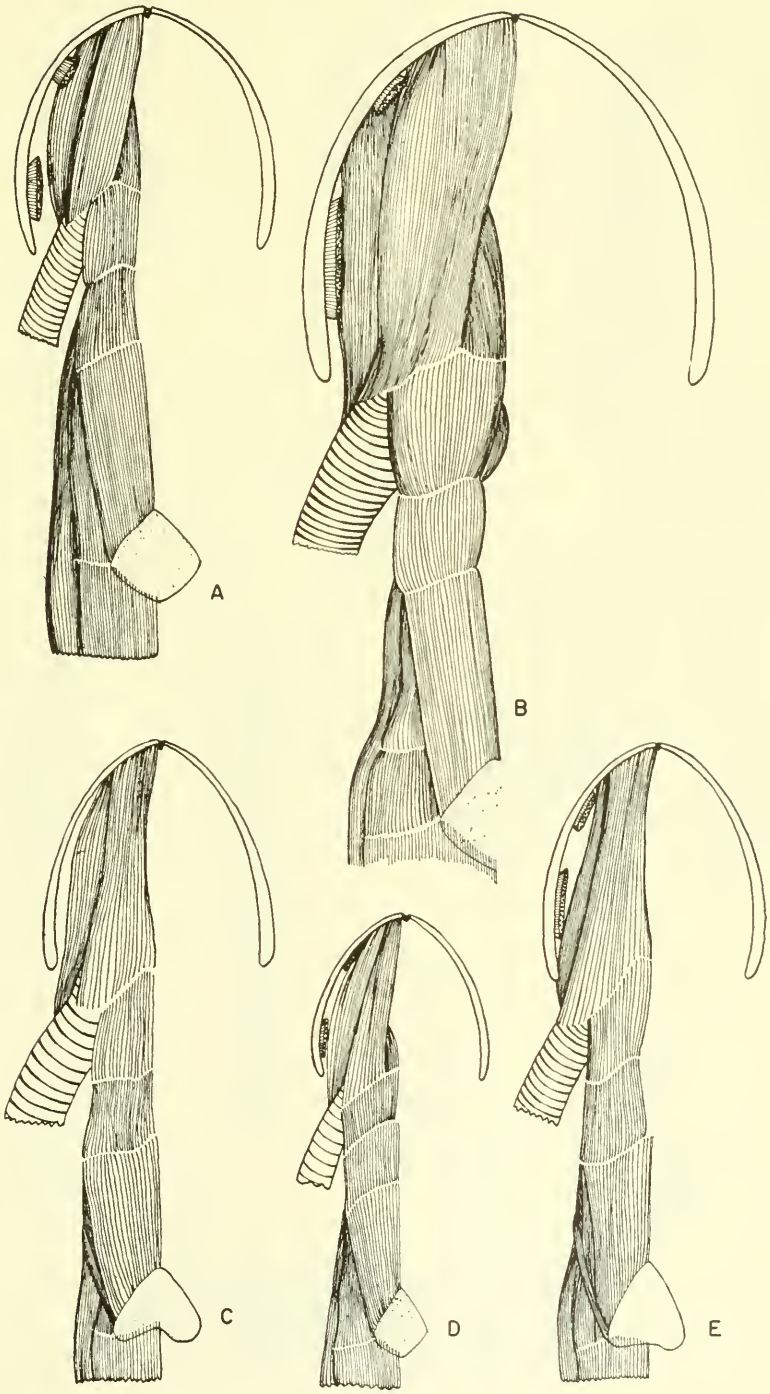


PLATE LXXII

FIG. A. *Bolitoglossa striatula* (Noble). Longitudinal throat muscles. E. H. T. No. 402. × 4.

FIG. B. *Lineatriton lineola* (Cope). Longitudinal throat muscles. E. H. T. No. 26583. × 7½.

FIG. C. *Thorius narisovalis* Taylor. Longitudinal throat muscles. E. H. T. No. 25041. × 10.

FIG. D. *Oedipina uniformis* Keferstein. Longitudinal throat muscles. E. H. T. No. 1021. × 5.

FIG. E. *Parvimolge townsendi* (Dunn). Longitudinal throat muscles. E. H. T. No. 31572. × 10.

FIG. F. *Pseudoeurycea rex* (Dunn). The deep throat muscles and the ceratohyals. E. H. T. No. 27281. × 5.

FIG. G. *Magnadigita macrinii* (Lafrentz). The deep throat muscles and the ceratohyals. Amer. Mus. Nat. Hist. No. A51823. × 4.

FIG. H. *Lineatriton lineola* (Cope). The deep throat muscles and the ceratohyals. E. H. T. No. 26583. × 7½.

FIG. I. *Bolitoglossa platydactyla* (Cuvier). Lateral view of head and throat muscles. E. H. T. No. 16321. × 2½.

PLATE LXXII

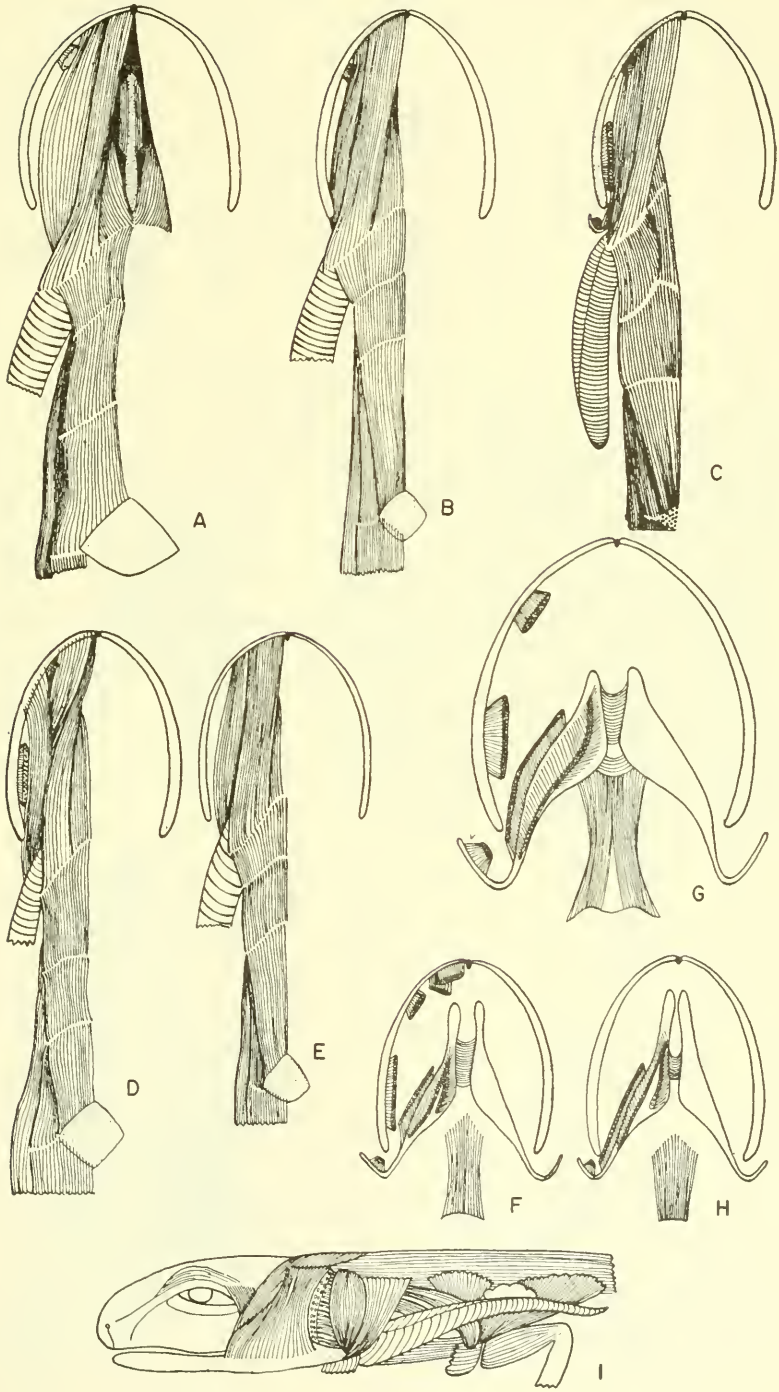


PLATE LXXIII

FIG. A. *Bolitoglossa rufescens* (Cope). The deep throat muscles and the ceratohyals. E. H. T. No. 18863. × 7½.

FIG. B. *Pseudoeurycea goebeli* (Schmidt). The deep throat muscles and the ceratohyals. E. H. T. No. 20301. × 4.

FIG. C. *Chiropterotriton abscondens* Taylor. The deep throat muscles and the ceratohyals. E. H. T. No. 1410. × 7½.

FIG. D. *Magandigita robusta* (Cope). The deep throat muscles and the ceratohyals. E. H. T. No. 25074. × 7½.

FIG. E. *Pseudoeurycea nigromaculata* (Taylor). The deep throat muscles and the ceratohyals. E. H. T. No. 24603. × 5.

FIG. F. *Bolitoglossa striatula* (Noble). The deep throat muscles and the ceratohyals. E. H. T. No. 402. × 4.

FIG. G. *Bolitoglossa platydactyla* (Cuvier). The deep throat muscles and the tongue. E. H. T. No. 16321. × 5.

FIG. H. *Pseudoeurycea cochranae* (Taylor). The deep throat muscles and the ceratohyals. E. H. T. No. 17727. × 5.

PLATE LXXIII

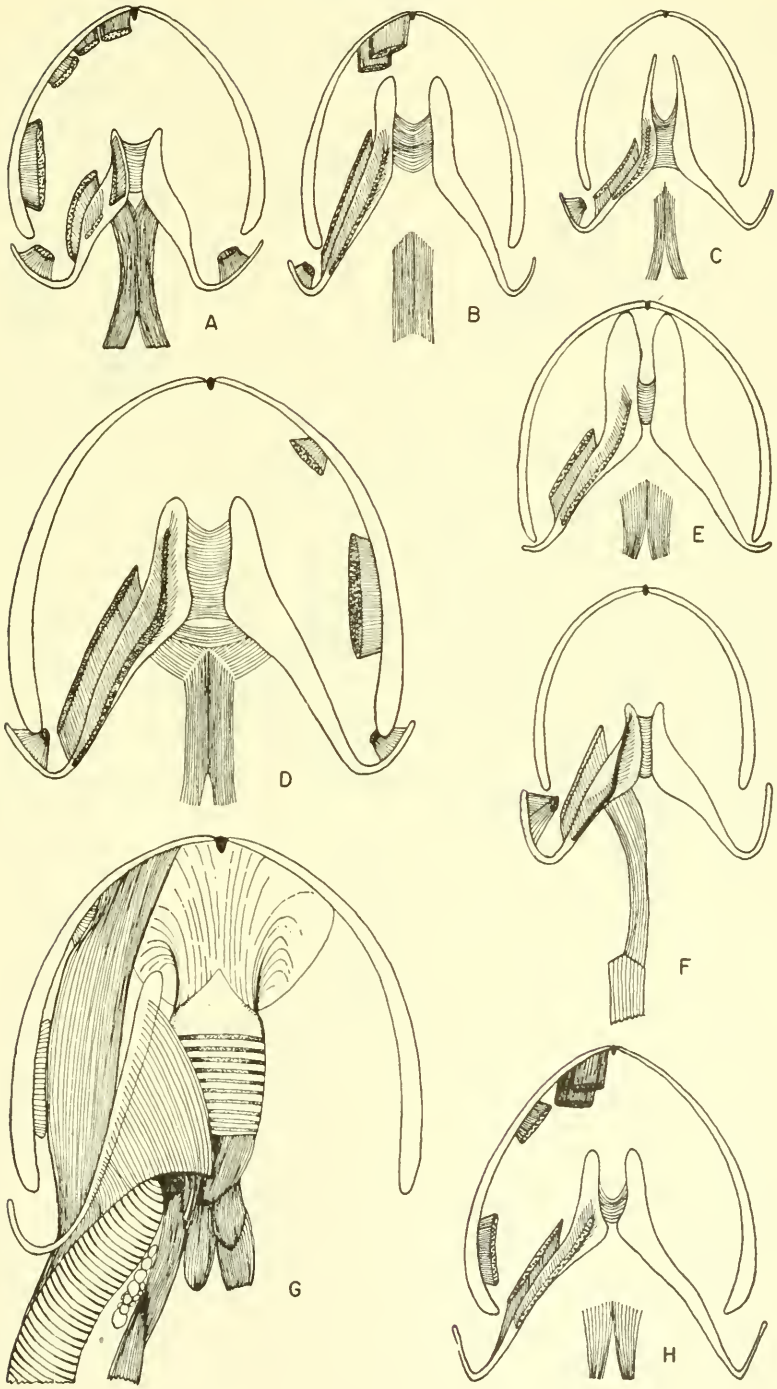


PLATE LXXIV

FIG. A. *Thorius narisovalis* Taylor. The deep throat muscles and the ceratohyals. E. H. T. No. 25041. × 10.

FIG. B. *Thorius macdougalli* Taylor. The deep throat muscles and the ceratohyals. Amer. Mus. Nat. Hist. No. A51800. × 10.

FIG. C. *Pseudoeurycea gigantea* (Taylor). The deep throat muscles and the ceratohyals. E. H. T. No. 28910. × 2½.

FIG. D. *Oedipina uniformis* Keferstein. The deep throat muscles and the ceratohyals. E. H. T. No. 1021. × 5.

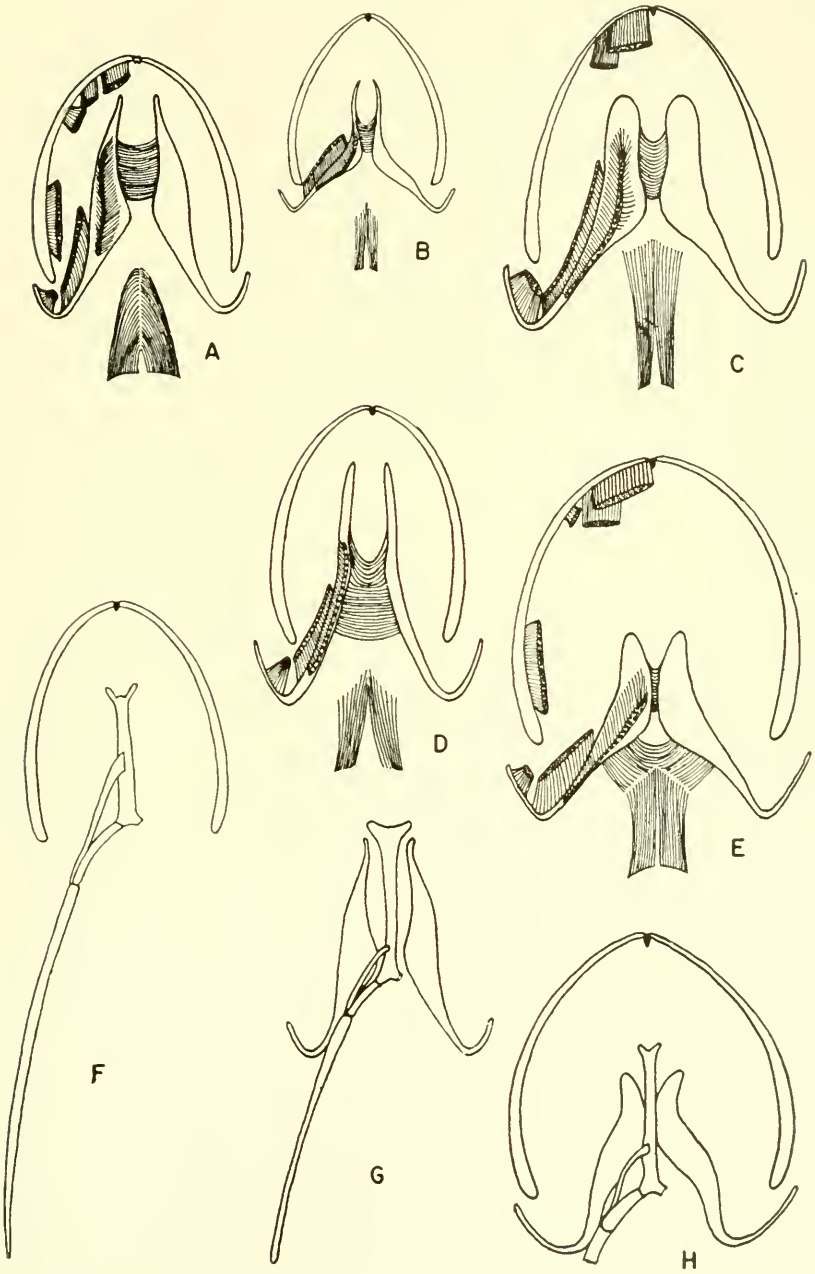
FIG. E. *Magnadigita subpalmata* (Boulenger). The deep throat muscles and the ceratohyals. E. H. T. No. 2111. × 5.

FIG. F. *Lineatriton lineola* (Cope). The hyobranchial apparatus. E. H. T. No. 26583. × 7½.

FIG. G. *Thorius narisovalis* Taylor. The hyobranchial apparatus. E. H. T. No. 25041. × 10.

FIG. H. *Bolitoglossa rufescens* (Cope). The hyobranchial apparatus. E. H. T. No. 18863. × 7½.

PLATE LXXIV



THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

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Geographic Variation in the Lizard *Eumeces anthracinus*

BY

PHILIP W. SMITH AND HOBART M. SMITH

ABSTRACT: Based on a study of 187 specimens of *Eumeces anthracinus* the authors recognize two subspecies, *anthracinus anthracinus* and *anthracinus pluvialis*. The former is distributed chiefly in the northern Appalachian Mountains, the latter having a wide range in the southern Appalachian Mountains, and west of the Mississippi River from eastern Kansas and Missouri south to northern Louisiana.

In 1946, one of us (H. M. Smith, 1946a, pp. 87-88) pointed out that the range of the coal skink, *Eumeces anthracinus* (Baird), appeared to be discontinuous, consisting of three geographically distinct populations: an eastern one extending from New York to Georgia, a second one in the Ozark Uplands, and a third in extreme southern Alabama and Mississippi. Attention was called to the fact that juvenal lizards from the Ozark area were known to differ in color and pattern from those in the Appalachian Mountains. The juvenal markings of the Alabama-Mississippi populations, however, were unknown. Tentative retention of the name *pluvialis* (Cope, 1880) was suggested for the southern and western populations, pending examination of the young lizards from the Alabama-Mississippi area and detailed comparison of specimens from the various portions of the known range.

We have recently examined all the material readily available and find that some of the above statements require revision. Two races are involved, differing in scutellation as well as in color and pattern of the juvenal lizards. Specimens from many localities between the areas previously known to be inhabited have been taken in recent years, however, indicating the range of the species to be more nearly continuous from New York to Kansas than indicated in the recent handbook of lizards (Smith, 1946b). Moreover, our data

show that specimens from the southern Appalachians are indistinguishable from Ozark specimens but are distinct from those in the northern Appalachians.

Our study is based on 187 specimens, slightly more than twice the number available to Taylor at the time of his admirable generic revision (Taylor, 1936) and from considerably more than twice as many localities. We are indebted to the following museum officials and collectors for the privilege of examining preserved material in their charge: S. C. Bishop, C. M. Bogert, B. C. Brown, F. R. Cagle, D. M. Cochran, A. F. Cook, H. Dowling, E. R. Dunn, J. A. Fowler, N. E. Hartweg, R. L. Hoffman, R. T. Hoskins, H. K. Gloyd, A. L. Loveridge, M. G. Netting, A. I. Ortenburger, G. L. Orton, C. H. Pope, E. C. Raney, K. P. Schmidt, and E. H. Taylor. We are also indebted to Drs. D. F. Hoffmeister and H. H. Ross for critical perusal of the manuscript. Abbreviations for the sources of material studied are as follows:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences at Philadelphia
BCB	Bryce C. Brown
CAS	Chicago Academy of Sciences
CM	Carnegie Museum at Pittsburg
CNHM	Chicago Natural History Museum
CU	Cornell University Museum of Natural History
FC	A. Fannye Cook
INHS	Illinois Natural History Survey
KU	University of Kansas Museum of Natural History
MCNP	Mammoth Cave National Park
MCZ	Museum of Comparative Zoology at Harvard
OU	University of Oklahoma Museum of Natural History
RLH	Richard L. Hoffman
TU	Tulane University Museum of Zoology
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
UR	University of Rochester Museum of Natural History
USNM	United States National Museum

The species was first described by Baird (1850, p. 294) from North Mountain near Carlisle, Pennsylvania. Cope (1875, p. 45) was the next to contribute to the knowledge of the lizard, recording the range of the species as "Pennsylvania to Texas, in mountains". Two years later in his address to the American Philosophical Society (Cope, 1877, p. 64), the same author mentions receiving a specimen of a variety of *Eumeces anthracinus* from Mobile, Alabama. Three years later (Cope, 1880, p. 19, footnote) this was described as the type of a new species, *Eumeces pluvialis*. Burt (1928, p. 50) expressed doubt of the validity of the latter species

and referred all Kansas specimens to *Eumeces anthracinus.* Taylor (*op. cit.*), having extremely few eastern specimens, was unable to separate the two forms and he also regarded Cope's name as a synonym. Clausen (1938, p. 6) mentioned differences in juvenal coloration and pattern and later Smith (1946a, *loc. cit.*) resurrected *pluvialis* as a subspecific name for the southern and western populations for reasons outlined in our introductory paragraph.

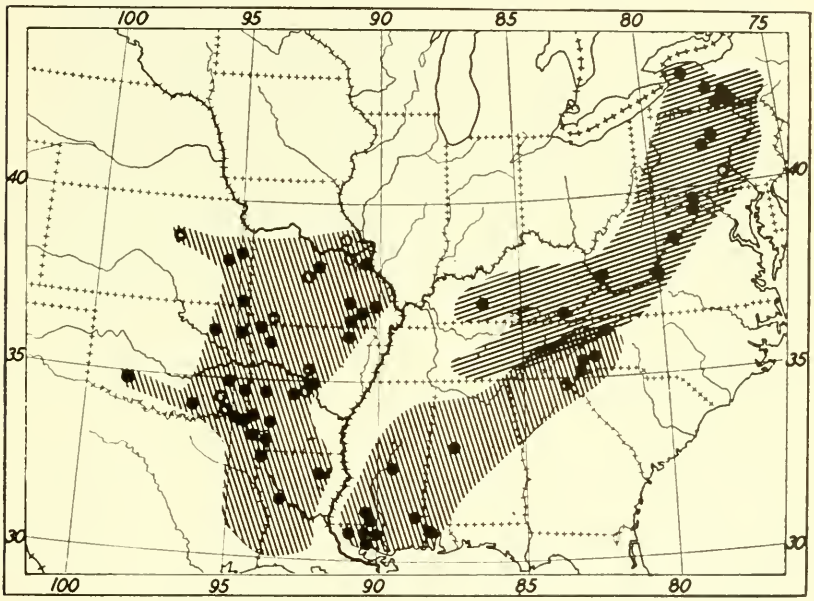


FIG. 1. Distribution of the subspecies of *Eumeces anthracinus.* Solid dots indicate specimens examined, open circles indicate literature records. Lines extending southwestward indicate the range of *E. a. anthracinus;* those extending southeastward indicate the range of *E. a. pluvialis.* Extension of the conjectured range (the hatched area) into areas from which no records are available is based upon apparent availability and accessibility of presumably suitable habitat. The presumed area of intergradation occupied by nearly exactly intermediate populations is indicated by the zone of overlapping (crossing) lines.

Eumeces anthracinus (Baird)

Diagnosis. A medium-sized skink of the *anthracinus* group of *Eumeces,* characterized by absence of postnasals, possession of a single postmental, moderately well-developed limbs which usually overlap when adpressed, a dorsolateral and lateral light line enclosing a dark brown stripe extending the length of the body, median light stripe if present not forking on head at neck, 23-30 scale rows, dorsal scales not widened.

KEY TO SUBSPECIES

1. Scale rows 23-26, av. 24.5, usually (81.1%) 25 or fewer; a continuous light line through posterior supralabials, or at least no evidence of spotting; frequently 7-6 supralabials or less (68.5% toward north, 47% toward south); usually no evidence of longitudinal dark stripes or rows of spots between dorsolateral light lines (66%); color and pattern in juveniles as in adults, *a. anthracinus*

Scale rows 24-30, av. 27.6, usually (99%) 26 or more; supralabials light-centered, sutures dark; usually (94.5%) 7-7 supralabials or more; usually one or more longitudinal dark stripes or rows of spots between dorsolateral light lines (65%); body of juveniles dark with stripes obscure or absent. . . . . *a. pluvialis*

Eumeces anthracinus anthracinus (Baird)

Plestiodon anthracinus Baird, Journ. Acad. Nat. Sci. Philadelphia, vol. 1, p. 294, 1850 (North Mountain, near Carlisle, Cumberland Co., Pennsylvania).
Eumeces anthracinus, Cope, Ann. Rep. U. S. Nat. Mus. for 1898, pp. 661-663, 1900 (part); Taylor, Univ. Kan. Sci. Bull., vol. 23, pp. 373-387, 1936 (part).
Eumeces anthracinus anthracinus, Smith, Univ. Kansas Publ. Mus. Nat. Hist., vol. 1, no. 2, p. 87, 1946.

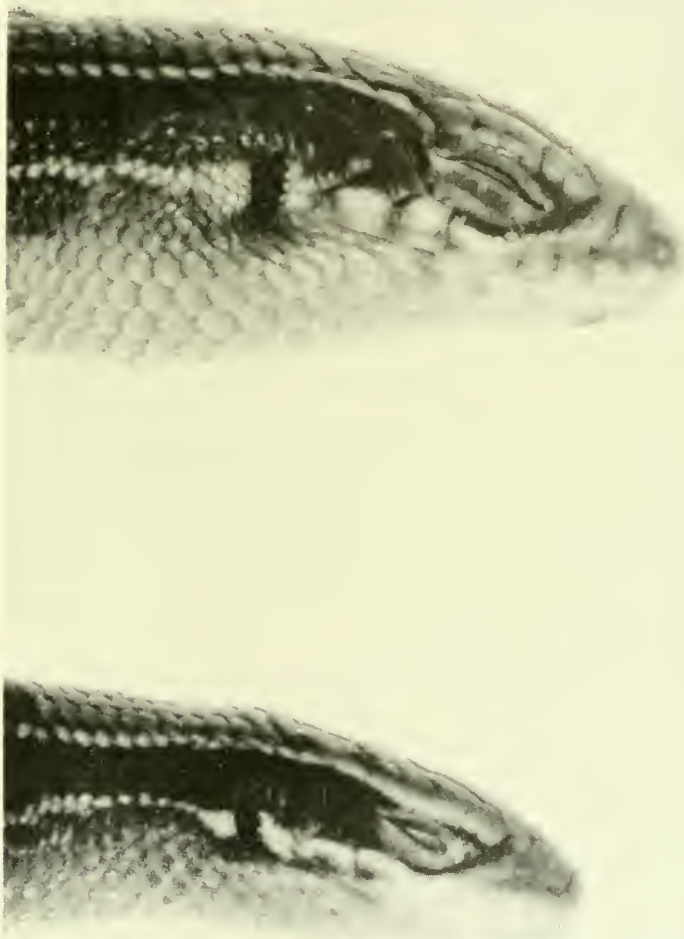
Type specimens. Five cotypes (USNM no. 3138) are in the U. S. National Museum, all in very bad condition. No data concerning collector or date of collection are available.

Range. Central and western New York from Lake Ontario south through montane Pennsylvania, Maryland, West Virginia, and Virginia to central Kentucky and northwestern North Carolina (Fig. 1).

Diagnosis. A subspecies of *E. anthracinus* with a broad, conspicuous black or brown lateral stripe bordered above and below with narrow light lines, the lower continuous through ear to the elevated loreal scales; six (51%) or seven supralabials; 23-26 (average, 24.5) scale rows at midbody; one (26%) or two (8%) pairs of dark lines or rows of dots between dorsolateral light lines; juveniles with markings much like adults.

Variation. Of 54 specimens examined, all are typical in the presence of a single postmental and the absence of postnasals. The number of scale rows at midbody varies from 23 to 26 with the following frequencies: 23, one; 24, thirty-two; 25, five; 26, nine. No geographic cline is evident in this feature of scutellation. In the number of supralabials, however, New York series show a higher frequency of specimens with a reduced number of supralabials. Thirty-eight specimens from New York show the following

variation: 7-7, 31.5%; 7-6, 10%; and 6-6, 58.5%. Sixteen specimens from the southern Appalachians (Pennsylvania to Central Kentucky) yield the following percentages: 7-7, 53%; 7-6, 14%; and 6-6, 33%. Slightly more than half the available specimens of this race thus possess six supralabials on each side of the head. Infralabials



Pl. LXXV. Lateral views of the head and neck of a specimen of the two subspecies of *Eumeces anthracinus*. Upper, *E. a. pluvialis*, UIMNH 16332, five miles east of Baxter Springs, Cherokee Co., Kansas, snout-ear length 8.8 mm. Lower, *E. a. anthracinus*, CU 3335, Connecticut Hill, Tompkins Co., New York, snout-ear length 7.5 mm.

are usually 6-6, occasionally five or seven on one side. Subdigital lamellae vary from 11 to 14.

The ground color dorsally is usually brown but approximately one fifth of the available specimens are light green. Most of the latter are large adults. The lateral stripes are most often dark brown or occasionally black in preserved specimens. In about 66% of the material at hand, the dorsal scales between the lateral dark bands are immaculate or the dorsolateral dark stripes are edged only with narrow light lines. Approximately 26% of the specimens have a narrow dark stripe or longitudinal row of dark spots bordering each of the light lines medially, and 8% have an additional pair of longitudinal rows of dark spots down the middle of the back. None has a middorsal light stripe. In almost all the available specimens the mental and adjacent scales are conspicuously lighter than the other head and ventral scales.

The largest specimen examined is 65.5 mm. from snout to vent with a head length of 11.2 mm. Several other specimens exceed 60 mm. from snout to vent. The head length/body length ratios range from 17% to 21%, averaging 19%. Relative tail lengths could not be determined inasmuch as very few preserved specimens have complete tails. Body length/leg length ratios were impossible to determine accurately without damaging the frequently brittle specimens. Leg lengths nevertheless appear to vary considerably, the legs overlapping (when adpressed) as much as the length of the longest toes in many specimens and in others the toe tips are separated by as great a distance. No apparent correlation occurs between leg length and sex.

Discussion. The absence of a marked color and pattern change from the time of hatching to maturity is an apparently significant character separating this race from the following subspecies. Clausen (*op. cit.*) describing a hatchling states: "It was 45 mm. long, of which the tail was 20 mm., and had the same pattern as the adult, but with the tip of the nose and sides of the head orange, the back olive black bordered by a narrow yellow stripe on each side, the side bands and legs deep black, and the tail blue." In preserved juveniles the upper lateral light stripe extends to the anteriormost supraocular (Pl. LXXV), and usually becomes obscure in most adults, disappearing first in the males as the jaw regions become orange or red.

The lower lateral light stripe provides another reliable character. It is interrupted only at the anterior edge of the ear or not at all,

and is readily discernible on the sides of the head of some of the largest specimens studied (60 mm. or more from snout to vent). Less than ten percent of our material is so mottled that the lower lateral head stripe is indistinguishable.

Material examined. Forty-five specimens, as follows: KENTUCKY.—*Bell Co.* (CAS 13904); *Edmonson Co.*: Mammoth Cave Ridge (MCNP 104). MARYLAND.—*Alleghany Co.* (ANSP 9433-4). PENNSYLVANIA.—*Clinton Co.*: Renova (USNM 38197); *Clearfield Co.*: Karthaus (CM 6). NEW YORK.—*Genesee Co.*: Bergen (CU 3718, 2552); *Ontario Co.*: Hemlock Lake (UR 978); *Tioga Co.*: 1 mi. N Candor (CU 2310); Prospect Valley (CU 2589, 2374, 2499 [4], UR 7609); *Tompkins Co.*: Caroline (CU 603); Connecticut Hill (CU 2311, 2540, 3577, 3616 [3], 1874, 3355, 3694, 2338, 3335 [3]); Slope above Mich. Creek (CU 2612); ¾ mile up valley from Danby Pond (CU 2541); Newfield Twp. (CU 2551 [2], 2239 [2]); Prospect Valley (UIMNH 15119); near Willseyville (CU 3161); 1½ mi. E Willseyville (UR 7278). VIRGINIA.—*Alleghany Co.*: Clifton Forge (RLH 419); 3 mi. NW Clifton Forge (RLH 71). WEST VIRGINIA.—*Hampshire Co.*: near Slanesville (CM 18358); *Logan Co.*: 2 mi. E Mallory (CM 16099); *Pendleton Co.*: 2 mi. above Franklin (CM 15482).

Other localities. Baird (*loc. cit.*) records the species from North Mountain, near Carlisle, Cumberland Co., Pennsylvania (type locality), and Clausen (1938, pp. 3-7) from Chemung Co., New York. Apparently the subspecies may be expected in the state of Tennessee, although records from there are not now known. Specimens are much to be desired from that state and also from Virginia, where intergradation with *E. a. pluvialis* presumably occurs. It is possible, although perhaps not probable, that the species occurs also in Ohio.

Eumeces anthracinus pluvialis Cope

Eumeces pluvialis Cope, Bull. U. S. Nat. Mus., no. 17, footnote p. 19, 1880 ("near Mobile, Alabama").
Eumeces anthracinus pluvialis, Smith, Univ. Kansas Mus. Nat. Hist. Misc. Publ., vol. 1, no. 2, pp. 87-88, 1946.
Eumeces anthracinus, Burt, Trans. Acad. Sci. St. Louis, vol. 26, no. 1, pp. 49-51, 1928 (part); Taylor, Univ. Kansas Sci. Bull., vol. 23, pp. 373-387, 1936 (part).

Type specimen. Cope's original type specimen (collected by Dr. Joseph Corson) has apparently been lost. Taylor (*op. cit.*) designated USNM no. 75291 (the only topotype then extant) as neotype of *E. pluvialis*. The latter specimen was collected by H. P. Löding.

Range. Western North Carolina to extreme northeastern Georgia and westward to southeastern Kansas and northeastern Texas (Fig. 1).

Diagnosis. A subspecies of *Eumeces anthracinus* differing from the typical subspecies by the greater number of scale rows at midbody (24-30, average 27.6); supralabials light-centered, sutures pigmented; seven supralabials (94.5%); body color dark in juvenal lizards; and dorsal markings frequently present between lateral dark bands.

Variation. Three of the 142 specimens examined (KU 8808, KU 23615, and MCZ 29313) are atypical, possessing two postmental scales (the presence of a single postmental is considered the most reliable single specific character). The specimens are remarkably similar in dorsal pattern and scutellation to occasional specimens of the southern races of *Eumeces septentrionalis.* In all three of the atypical *E. a. pluvialis*, however, the anterior postmental is very short (approximately 1/5 the length of the posterior scale). Other characters (see discussion under Phylogeny) reliably allocate the specimens with their proper species. Moreover, two of the three aberrant specimens (KU 8808 and MCZ 29313) are from Arkansas, which is east of the known range of *E. septentrionalis.*

The number of scale rows at midbody ranges from 24 to 30 with the following frequencies: 24, one; 25, none; 26, twenty-three; 27, six; 28, fifty-five; 29, three; and 30, eight. The one specimen with 24 scale rows (USNM 75291) is the neotype designated by Taylor. Selection of an aberrant specimen as neotype is unfortunate; but as has been pointed out, USNM 75291 was the only topotype available at that time. In head pattern and number of supralabials the neotype agrees with other western specimens. Of the 112 specimens from which scutellation data could be taken, 105 have seven supralabials on each side, five have six on a side, and two have eight on each side. Infralabials are almost invariably six on each side. Subdigital lamellae range from 12 to 16. The frontonasal varies considerably in size, perhaps averaging somewhat larger in this race than in the former subspecies but the difficulty in measuring relative size renders it useless as a key character.

Ground color dorsally in adults and subadults is brown or light green as in the preceding subspecies but the dorsal scales between the lateral dark bands are more often marked. Chief pattern types and their percentages are as follows: dorsal scales immaculate or inner surfaces of lateral bands margined with narrow light lines, 35 percent; a narrow longitudinal dark stripe or row of black dots

bordering the medial edge of each light line, 27 percent; four narrow longitudinal dark stripes or rows of black spots, 5 percent; and a middorsal light stripe from occiput onto base of tail, 33 percent.

The largest specimen examined is 64.8 mm. from snout to vent with a head-length of 12 mm. A number of other specimens exceed 60 mm. in snout-vent length. Head length/snout-vent length ratios in adults range from 17 percent to 22 percent, averaging 20 percent. Variation in leg length seemingly parallels that in *Eumeces anthracinus anthracinus* with no apparent sexual correlation.

Discussion. Coloration and pattern of living juveniles have not been adequately described. Gloyd (1928, p. 120) and Burt (1928, p. 49) both describe the black color and blue tails. Gloyd also mentions the red tint on the chin and sides of the head. Newly hatched preserved specimens have light infralabials, rostral, mental, and postmental, all in sharp contrast to the dark body color; seven conspicuous light spots along the supralabials; white loreals; a white dash on the supraocular; a small light spot at the anterior edge of the ear; a light spot on each internasal; and a crescent-shaped light mark on each frontonasal (Pl. LXXV).

These light spots (presumably red-orange in life) are apparently lost in the following order: frontonasals, internasals, loreals, supraoculars, anterior edge of ear, and anterior supralabials. The light spots on the posterior supralabials, although losing their contrast as they become gray, gray-green, or red (in males), are still evident in large adults. They are separated by pigmented labial sutures, thus providing a ready character to separate this from the typical subspecies. Somewhat larger juveniles (30-35 mm. from snout to vent) retain the conspicuous light-centered supralabials but exhibit the body pattern and color of the adult lizards. The middorsal light stripe does, however, appear to be most frequent in this age group, often being obscured in the larger specimens.

Although the ontogenetic change in color and pattern (the general obscuring of the light spots on the head accompanied by an increasing sharpness of the lineate body pattern) is rather gradual, it is nevertheless distinctive compared with the remarkably close resemblance of juveniles and adults of the typical subspecies. The black body color noted by Burt and Gloyd in Kansas hatchlings may have been over-emphasized by them and others, as may also have been the distinctive linear pattern noted by Dowling (1950, p. 235) in an Alabama specimen, since our own fresh material (SE Missouri) exhibits neither extreme but does show longitudinal

stripes, when proper lighting is used, despite the very dusky ground color.

Remarks. A series of eight eggs laid in captivity by a specimen of *E. a. pluvialis* from 1 mile north of Greer, Oregon Co., Missouri (UIMNH 15122), varied at deposition from 7 mm. to 7.8 mm. in width, and 12 mm. to 13 mm. in length. The width at hatching had increased to 11-12 mm., the length to 16.2-18 mm. Of special interest is the fact that whereas the length increased rather uniformly throughout the developmental period, the width increased as much

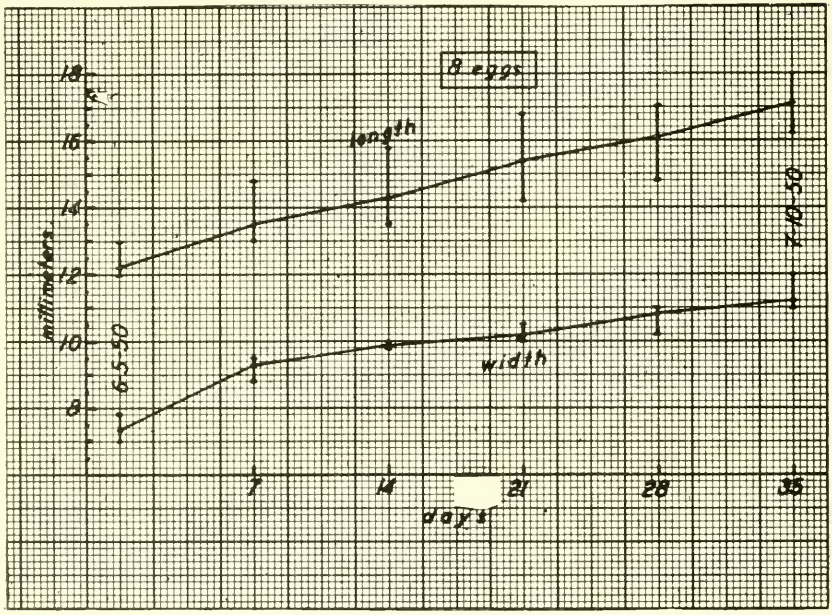


FIG. 2. Post-depositional changes in dimensions of 8 eggs of *Eumeces anthracinus pluvialis*. Range of variation is shown by vertical lines; averages are connected by a continuous diagonal line.

in the first seven days as it did during the ensuing 28 days before hatching. The accompanying graph (Fig. 2) depicts these changes.

Material examined. One hundred and forty-two specimens, as follows: ALABAMA.—*Mobile Co.:* Mobile (USNM 75291, neotype); *Tuscaloosa Co.:* 8 mi. NE Tuscaloosa (UMMZ 98631, 98633). ARKANSAS.—*Benton Co.:* 2½ mi. N Sulphur Springs (UMMZ 60112, INHS 5024-5); *Garland Co.:* Hot Springs (CNHM 29166-71); *Hempstead Co.:* (UMMZ 84174); *Lafayette Co.:* (KU 8803-9); *Lawrence Co.:* Imboden (AMNH 65797; CM 4708; KU 8219, 8221-3, 8229; MCZ 29312-8; TU 4969-70, 4973-4, 4981, 4989; UR

1422 [3], 45); 5 mi. SW Imboden (KU 8225-8, 8230, 8952-3, 8840); *Madison Co.:* Combs (USNM 118516); *Montgomery Co.:* 3 mi. W Oden (USNM 99545); *Pulaski Co.:* NW Little Rock (CM 25136, 25158); 10 mi. NW Little Rock (KU 22895); *Sevier Co.:* DeQueen (CNHM 3514). Kansas.—*Anderson Co.:* (KU 742); *Cherokee Co.:* 4½ mi. E, ½ mi. N Baxter Springs (UIMNH 15120; KU 24413); 7 mi. E Baxter Springs (KU 23615); 5 mi. E Baxter Springs (UIMNH 15120, 16332); 2½ mi. W Galena (AMNH 44929-31); 3 mi. S Galena (KU 23029); 2 mi. N Ellerville (UIMNH 15123); *Dickinson Co.:* (KU 744); *Franklin Co.:* (KU 8217; UMMZ 68453 [5], 66924, 100864); *Miami Co.:* (UMMZ 68450-2 [7]); 3 mi. E Fontana (UIMNH 15568). Louisiana.—*Caddo Pa.:* Gayle (KU 8212); 7 mi. W Plain Dealing (TU 3744-5); Rodessa (TU 739); *East Feliciana Pa.:* 3 mi. W Clinton (TU 10672); *Natchitoches Pa.:* Steep Hill Creek (KU 24577); *Ouachita Pa.:* Monroe (TU 4977); *St. Tammany Pa.:* 5 mi. S Enon (TU 5908); *Tangipahoa Pa.:* Fluker (TU 4817); *Washington Pa.:* 10 mi. W. Bogalusa (TU 4821). Mississippi.—*Greene Co.:* Gaines Creek (UR 2470); *Leake Co.:* 12 mi. SE Carthage (CAS 6280); *Lincoln Co.:* 2½ mi. NE Summit (USNM 116457); *Pike Co.:* (FC 2054). Missouri.—*Carter Co.:* near Van Buren (UMMZ 68936); *Jefferson Co.:* Pevely (USNM 56905); *Miller-Pulaski Co. line:* Rubidaux Creek (UMMZ 68744); *Oregon Co.:* 1 mi. N Greer (UIMNH 15122, 16333-40); *Shannon Co.:* Current River (UMMZ 90465); *Wayne Co.:* Sam A. Baker State Park (UMMZ 95818). North Carolina.—*Buncombe Co.:* Asheville (UIMNH 15121); *Heywood Co.:* Pisgah Forest (UMMZ 52583; MCZ 12821); *Transylvania Co.:* Looking Glass Creek (USNM 61309). Oklahoma.—*Adair Co.:* 5 mi. S Kansas (UMMZ 81379); *Bryan Co.:* near Durant (OU 9352); *Tulsa Co.:* Tulsa (UMMZ 97446); *Le Flore Co.:* 3½ mi. NE Page (OU 16739); 5 mi. E Page (OU 26917); *Latimer Co.:* 1 mi. N Wilburton (OU 11498, 11703-4, 11711); 2 mi. NE Wilburton (OU 11659); 2 mi. NW Wilburton (OU 11559); 2½ mi. N Wilburton (OU 11268, 11329); 2½ mi. N, 1½ mi. E Wilburton (OU 11096, 11233-4); *McCurtain Co.:* near Idabel (OU 23566, 23568); Beavers Bend State Park (OU 26037); 14 mi. SE Broken Bow (OU 17288, 17349); 14 mi. E Broken Bow (OU 17567-8). Texas.—*Bowie Co.:* W and SW Maud (BCB 5754).

Other localities. Specimens have been recorded from the following localities not represented by specimens examined. Arkansas.—*Faulkner Co.:* 7 mi. W Conway (Dellinger and Black,

1938, p. 15); *Saline Co.:* (Taylor, *op. cit.*, p. 386). GEORGIA.—*Rabun Co.:* Mountain City (McCauley, 1940, p. 50). MISSOURI.—*Barry Co.:* Rockhouse Cave (Taylor, *op. cit.*, p. 386); *Franklin Co.:* (Hurter, 1911, pp. 142-143); *LaClede Co.:* (Hurter and Strecker, 1909, p. 23); *Warren Co.:* Warrenton (Hurter, 1911, pp. 142-143). OKLAHOMA.—*Comanche Co.:* Wichita Mts. (Ortenburger, 1926, p. 138); *Pushmataha Co.:* (Ortenburger, 1926, p. 95).

This subspecies apparently is to be expected in South Carolina, Tennessee, and Illinois, although records from those states are not now known. Specimens are much to be desired from these and from certain other states, especially North Carolina, Georgia, Alabama, and Mississippi.

Intergradation. The recognition of intergrading specimens is rather difficult as a result of the overlapping nature of subspecific characters and the fact that seldom is there more than one specimen available of this uncommon lizard from a critical locality. We believe that when possible (other things being equal) the boundary line between the two subspecies in the intergrading areas should be that indicated by transition in the color, pattern, or some other quite obvious feature, although other characters may not be intermediate. We have arbitrarily selected the condition of the supralabial markings as the feature by which specimens (or populations, when adequate series are available) from intermediate areas are allocated. In this feature two of the four available specimens from western North Carolina (MCZ 12821 and UMMZ 52583) are intermediate. The remaining two specimens, although mottled on the posterior supralabial region, appear much closer to *E. a. pluvialis.* All four specimens have 26 scale rows at midbody whereas 75% of a random sample of the subspecies would be expected to have 27 or more scale rows. Regrettably, we have not been able to locate the specimen reported from Rabun County, Georgia (McCauley, 1940, p. 50). The single specimen available from central Kentucky (MCNP no. 104) is rather puzzling, possessing 26 scale rows at midbody and showing a tendency toward darkening of the labial sutures. Until a series is availale, however, we regard the Kentucky specimens as *E. a. anthracinus.*

Phylogeny and zoogeography. Phylogenetic speculations regarding two subspecies often are not warranted. In the present case we are tempted to suggest that *Eumeces anthracinus pluvialis* is the more primitive form, inasmuch as (1) a median light stripe occurs frequently in half-grown specimens (occurrence of five

stripes is undoubtedly an ancestral condition for members of the four-lined group), (2) there are more numerous scale rows, and (3) there are more numerous supralabials.

Of interest is the extraordinary similarity mentioned previously of *Eumeces septentrionalis* (especially *E. s. pallidus* and southern *E. s. obtusirostris*) and *E. anthracinus pluvialis*. The similarity extends to scutellation as well as pattern and color. The two species differ most conspicuously in the number of postmentals (one in *E. anthracinus*, two in *E. septentrionalis*) and also in the relation of the lateral light line to the ear (passing through the ear in the former, above in the latter), in extent of light area on ventral surface of the head (mental area only in the former, entire area in the latter), and in width of the subcaudals (relatively wide in the former, narrow in the latter). The similarities are sufficient in number, however, to indicate (1) a close relationship of the two species, and (2) an apparent derivation of *E. anthracinus* from ancestors similar to *E. s. obtusirostris*.

Throughout most of its range *E. a. pluvialis*, despite a certain apparent flexibility of choice, seems to be restricted fairly closely to humid habitats of coniferous, oak, or mixed oak-coniferous forests in hilly terrain. Virtually all of the available area covered by such forests, excluding zones eliminated by obvious temperature and/or humidity factors, are inhabited by the subspecies. Exceptions will be accounted for in the following discussion. In Kansas specimens are found in oak-hickory woods of creek slopes; in Missouri and Arkansas the same and the oak-pine habitat (Shantz and Zon, 1924) are occupied in and near the Ozark plateau, almost wholly south of the Missouri River. In neither state has the species been found in the eastern bottomlands. In Texas, Louisiana, Mississippi, and Alabama the species seems to be wholly restricted to the longleaf pine habitat.

It may be assumed that temperature limits the northward dispersal of *E. a. pluvialis*. Westward dispersal is obviously limited in central Kansas and Oklahoma by the tall grass prairie, although the species apparently extends up certain river valleys far into this otherwise unfavorable region. The record for Dickinson County, Kansas, is an example of such extension. The one from Wichita Mts., Oklahoma, may be another example, but it is open to grave doubt inasmuch as the specimen on which the record was based cannot now be found. Possibly it actually represented the confusingly similar *E. septentrionalis obtusirostris*.

In eastern Texas the westward limit of range apparently does not reach the prairie. Although the entire eastern quarter of Texas (oak-pine and oak-hickory) appears to be a suitable habitat, the species has not been found there. The failure of *E. a. pluvialis* to expand its range westward in Texas may be due to the occurrence in that area of an apparent competitor, *E. septentrionalis*, whose range is overlapped nowhere to any degree by that of the adjacent *E. anthracinus*.

On the east the range of *E. a. pluvialis* is apparently restricted by the extensive bottomlands of the Mississippi Valley, which may provide a barrier across which the species does not and has not passed (north of Louisiana). In Louisiana the subspecies has been enabled to cross the valley of that river, and subsequently to extend its range eastward to the Appalachian Mountains, probably because of the Pleistocene alterations in the Mississippi river channels.

The range of *E. a. anthracinus* appears to be limited to the chestnut-chestnut oak-yellow poplar association, which covers vast areas north of Georgia and west of the Mississippi. Fingers or spots extend the range into western New York in suitable areas surrounded by the much more extensive and apparently unsuitable beech-maple habitat. To the east the form is apparently limited by the bottomlands of the Ohio and Tennessee rivers, which seemingly prevent infiltration into otherwise suitable areas of Ohio, eastern Kentucky, and eastern Tennessee. To the south the subspecies meets *E. a. pluvialis*.

The point of contact of the ranges of these two forms is the most perplexing problem presented by their distribution. It might be expected that the area of intergradation would coincide with an obvious ecotone, but such is not the case. The most obvious break in environmental conditions is in Georgia, for the chestnut-chestnut oak-yellow poplar habitat there meets the long-leaf pine habitat. It would be reasonable therefore to expect Georgia and North Carolina specimens to resemble the northern individuals, but they do not. They appear to represent more or less typical *E. a. pluvialis*. We believe it a foregone conclusion that some differences in environment were at least passively instrumental in effecting the differentiation of the two subspecies, producing an at least partial isolation. Since there is no correlation in the present area of contact (at least in the more obvious environmental factors such as vegetation, temperature, soil, and humidity as depicted in available maps), we assume that both subspecies formerly occupied more

restricted areas, and that *E. a. pluvialis* has, for reasons unknown, spread more rapidly than *E. a. anthracinus* and entered the habitat of the latter before *E. a. anthracinus* expanded fully within the habitat available to it.

The Mississippi River valley apparently bisects the range of *E. a. pluvialis*. The isolation has not as yet, apparently, been instrumental in facilitating differentiation of taxonomically distinguishable populations. There is reason to believe, moreover, that other sets of populations, of both subspecies, are as widely separated as the pair indicated on the map (Fig. 1). The hiatus depicted in the map is, however, virtually a certainty; the others are not obvious and can be verified, if they exist, only by much more extensive investigation.

We do not assume that postulations here made are necessarily correct. A full explanation of the distribution of this species and its subspecies will require extensive field work. Entirely too few facts are known at present to permit dogmatic conclusions regarding range, habitat, and phylogeny.

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The Salamanders and Caecilians of Costa Rica

BY

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ABSTRACT: The known caecilians and salamanders of Costa Rica are treated in this paper. The caecilians (Gymnophiona) are represented by two genera and three forms (species and subspecies). The salamanders are represented by six genera and twenty-seven species. In the latter group the following are described as new: *Magnadigita pesrubra, Magnadigita torresi, Magnadigita cerroensis, Oedipina bonitaensis, Oedipina cyclocauda, Oedipina longissima, Oedipina gracilis, Oedipina pacificensis* and *Oedipina inusitata.*

The salamander fauna is obviously an impoverished one, since, of the four families and eighteen genera occurring in Mexico, only one family and five genera reach Costa Rica. A single endemic genus, *Haptoglossa,* is known.

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INTRODUCTION

In the spring of 1947, I received an invitation from the Director of the National University of Costa Rica to spend the summer in Costa Rica studying the herpetological faunas of the country. It was hoped that one result from the journey would be the preparation of a publication that might serve as a taxonomic aid in the further study of the rich fauna of the country. I accepted the invitation with alacrity and was ready to leave on June 18. I was joined at this time by Richard C. Taylor, likewise interested in making a herpetological collection.

After an uneventful journey by air and a short delay in obtaining necessary permits, we found ourselves ready to begin our collecting on June 24. From this date until September 7, the greater part of our time was spent in the field.

Together we sampled the faunas in four principal areas. These were: the general area about Turrialba and the farm of the Inter-American Institute of Agriculture; the region about the American Cinchona Plantation at Isla Bonita on the eastern slope of Volcán Poás; the summit and western slope of the high peak, Cerro de la Muerte, in the Cordillera de Talamanca; and the lowland area northeast of Volcán Turrialba, at Los Diamantes.

Several subsidiary localities were visited and a few forms not found in the four major areas were acquired. For greater details of the journey and collecting, see my article, "A Brief Review of the Snakes of Costa Rica." Univ. Kansas Sci. Bull., vol. 34, pt. 1, 1951, pp. 1-188.

I wish especially to acknowledge my appreciation to my official host, Prof. Reubén Torres Rojas who contributed much to the success of my journey; and to Dr. Ralph H. Allee, the Director of the Inter-American Institute of Agriculture at Turrialba who permitted us to make the place our headquarters, and to use the facilities of the Institute to further our work.

A number of other persons helped us in many ways, among whom are: Dr. Fernando Baudrit, Rector of the University; Dr. Frederick Wellman, Mr. James Forman, Mr. David Allee, of the Inter-American Institute of Agriculture; Captain Hope, Mr. Deal Thornton, of the American Cinchona Plantation; Mr. Virgil Cave of the Pan-American Highways; Prof. Marco Tullio Pacheco of the National Museum; and Mr. Wallace E. Manis, Director of the rubber plantation at Los Diamantes.

The study here presented is based chiefly on the collections obtained by me together with those made by Richard C. Taylor, who has kindly placed his material at my disposal for study.

History of Literature and Collections

The first salamander to be described from Costa Rica was *Oedipina uniformis* Keferstein (1868). It was based on a specimen collected by von Seebach, and presumably lacking specific locality data. Almost at the same time another species was described as *Opheobatrachus vermicularis* Gray (1868), a species likewise without specific locality data. Certain subsequent workers have regarded the two species as synonymous; nevertheless, there is considerable evidence that such is not the case, and that two species are concerned. However, they are congeneric and the older generic name (by a few weeks only) is *Oedipina*.

The report by Edward D. Cope (1875) on the William Gabb herpetological collection made in the southeastern part of the country and on Pico Blanco, contains mention of one caecilian and two species of salamanders. These are listed as follows: *Siphonops mexicanus* Duméril and Bibron, from "near the coast at Limón"; *Opheobatrachus vermicularis* Gray, three specimens, one specimen from Pico Blanco, 6000 ft.," and "two other specimens are from the lower country twenty miles from the coast"; and *Oedipus*

morio? "a partly preserved specimen" from the eastern slope of Pico Blanco. It is surprising that the caecilians and salamanders in this early collection, so rich in reptiles and other amphibians, should have been so meagerly represented.

In 1877 Cope reported two new species of caecilians, *Siphonops proximus* and *Siphonops simus,* each lacking specific locality data. The first was collected by William M. Gabb; the second was sent by Dr. von Frantzius who may or may not have been the collector. Later (1879) Cope reported a specimen of *Oedipus morio* from Cartago, collected by Don José Zeledón (he had previously [1875] listed this species with a question). In 1894 he described from a single specimen the large species *Oedipus robustus* "from the Faldas of the volcano Irazu, from J. P. Cooper." He states that he is indebted to the Museo Nacional of San José for the opportunity of examining the described material.

Dr. George A. Boulenger (1896) described *Spelerpes subpalmatus,* from La Palma. This specimen was included in the herpetological collections made for the British Museum by Mr. C. F. Underwood.

No further new species were described until 1911, when Dr. Leonhard Stejneger described as new a small salamander from La Estrella, southeast of Cartago, under the name *Spelerpes picadoi.* The types were collected by Sr. C. Picado T., and presented to the U. S. National Museum.

In a work, treating of a collection from Nicaragua, Dr. Gladwin K. Noble (1918) described a new species of salamander, *Oedipus striatulus,* with the type locality Cukra, Nicaragua. He mentions a paratypic specimen from Turrialba, Costa Rica.

Dr. Emmet Reid Dunn described *Oedipina alfaroi* in 1921 from Zent, Costa Rica, this being the third species of the long-tailed, long-bodied forms to be recognized. Later Dunn (1924) described *Oedipus colonneus* from La Loma, Bocas del Toro, Panamá, a species which I have found to occur also in eastern Costa Rica. Dunn's important work on the plethodontid salamanders appeared in 1926. In this he reports the known salamander fauna of the country at that date. In this work considerable revisionary work was done, but unfortunately the various genera were lumped together under the preoccupied generic name *Oedipus,* thus often obscuring the true relationships of the species. He lists *Oedipus salvinii* from Marivalles, *Oedipus platydactylus* (based on an earlier record by Günther [1902] of *Spelerpes variegatus* from San Carlos) and *Oedipus lignicolor* from Sarapiqui. Dunn interpreted

certain previous questionable reports as follows: *Spelerpes brocchi* reported by Boulenger (1898) is placed in the synonymy of *Oedipus robustus;* Cope's (1875) record of *Oedipus morio* is referred to *Oedipus subpalmatus* (Boulenger) and *Oedipus variegatus* to *Oedipus lignicolor* (Peters). Dunn synonymizes *Haptoglossa pressicauda* Cope with *Oedipus uniformis* Keferstein.

It is highly probable that certain species as treated by this author are to be regarded as composite species, notably *Oedipus uniformis* and *Oedipus subpalmatus.*

Another work that should be mentioned, although in certain cases the identity of species may be questioned, is Albert Günther's Biologia Centrali-Americana; Reptilia and Batrachia, published between 1885-1902. The section on the Batrachia dealing with the caecilians and salamanders appeared between December, 1901 and May, 1902. The following species are listed from Costa Rica:

Spelerpes bocourti. From La Palma (1600 meters), and Cariblanco. (This species has been referred to the synonymy of *Magnadigita robusta.*)

Spelerpes subpalmatus. This is composite since certain of the type series is reported by Dunn as being, in the opinion of Boulenger, *Oedipus picadoi.*

Spelerpes morio. This seemingly is based on Cope's (1879) report.

Spelerpes robustus. This is based on Cope's (1894) description.

Spelerpes variegatus. He states "A specimen from this locality [San Carlos, Costa Rica, Underwood, coll.] named *Spelerpes morio,* is in the Natural History Museum." This specimen is believed by Dunn (1926) to be *Oedipus platydactylus.*

Spelerpes uniformis. Costa Rica, La Palma, 1600 m. altitude, Biolly, collector; and Bebedero and Irazú, Underwood, collector (several specimens, probably composite).

Gymnopis multiplicata. A specimen from Cariblanco, Underwood and Biolly collectors. He places *Siphonops simus* Cope as a synonym.

Gymnopis proxima. Based on Cope's (1877) record.

A report by Otto Wettstein, 1934, on a collection made in Costa Rica in 1930 contains records of twelve specimens of salamanders. The species are: *Oedipus subpalmatus,* 10 specimens from Volcan Irazú; *Oedipus picadoi,* La Caja near San José; and *Oedipina uniformis,* "Carrillo am Rio Sucio." The identification of these species was made, at least for the most part, by K. P. Schmidt.

Two papers dealing with the salamander collection made by Richard C. Taylor and me have been published. The first, Taylor (1948) describes *Chiropterotriton abscondens* and *Oedipina syndactyla,* both from the eastern slope of Volcán Poás. The second (1949) makes a hasty review of the known fauna, and describes *Magnadigita nigrescens, Bolitoglossa palustris, Parvimolge richardi,*

and *Oedipina serpens*. As these species are treated in the present paper, no further comment is made at this time.

The collections made by us and available in the present study total something more than 650 specimens—a number probably larger than has been obtained in past collecting—representing 22 forms, here considered as species.

SALAMANDERS

Order CAUDATA Oppel

Caudata Oppel, Ordnung, Familien und Gattungen der Reptilien, 1811, p. 72.

Suborder Plethodontoidea

Plethodontoidea Smith and Taylor, U. S. Nat. Mus. Bull. 194, 1948, p. 16.

family plethodontidae Gray

Plethodontidae Gray, Catalogue of the Batrachia Gradientia of the British Museum, 1850, p. 31 (*part.*).

The salamanders of Costa Rica are representatives of one family and of six genera. That the fauna is an impoverished one is evidenced by the fact that of the four families and the eighteen genera occurring in Mexico, only one family and five genera extend to Costa Rica; and of these, two genera are known to reach Panamá and the mainland of South America. A single genus *Haptoglossa,* with a single species, is known to be endemic in Costa Rica (possibly it will be found to occur also in Panamá since the type locality is in the southwestern part of Costa Rica, not far from the Panamá border). The other genera are represented by several species as follows: *Oedipina* 11; *Magnadigita* 6; *Bolitoglossa* 5; *Chiropterotriton* 2; and *Parvimolge* 1. The distribution of the six genera is as follows:

Bolitoglossa. A genus whose northern range reaches the State of Tamaulipas, Mexico, with representatives of both of the major groups present. It likewise has several representatives of the same two groups in Costa Rica, both of which extend into South America.

Chiropterotriton. A highland genus extending north to Tamaulipas, has two representatives in the mountains of Costa Rica.

Parvimolge. This genus has one species in Veracruz, and another representative in Costa Rica. Collecting in the intervening territory will probably eventually bring to light other species of this group of diminutive salamanders.

Magnadigita. This genus, entering Mexico in Chiapas and Oaxaca, has several representatives in Costa Rica.

Oedipina. A single species of this genus is known to have entered

Mexico, this in the state of Chiapas only. The genus has a number of representatives in Costa Rica and certain ones extending beyond into South America.

Two Mexican genera, *Thorius* and *Pseudoeurycea,* conspicuous in the fauna of the Mexican Plateau, have no known representatives that reach as far southward as Costa Rica. The attached table of known Mexican and Central American genera shows the diminution of the number of genera as one moves southward.

DISTRIBUTIONAL TABLE OF CAECILIAN AND SALAMANDER GENERA FROM MEXICO AND SOUTHWARD

	Western Mexico	Mexican Plateau	Eastern Mexico	Southern Mexico	Guatemala	Honduras	Salvador	Nicaragua	Costa Rica	Panama	Colombia	Venezuela	Peru	Brasil
Caecilia										×	×	?	×	×
Dermophis			×	×	×	×	×	×	×	×				
Gymnopis			×	×	×	×		×	×	×	×			
Siren			×											
Bathysiredon		×												
Siredon		×												
Rhyacosiredon		×												
Ambystoma	×	×	×											
Taricha	×													
Diemyctylus			×											
Thorius		×	×	×										
Ensatina	×													
Batrachoseps	×													
Aneides	×													
Pseudoeurycea		×	×		×									
Chiropterotriton		×			×	×			×					
Magnadigita				×	×	×		×	×	×	×	×	×	?
Bolitoglossa*			×	×	×	×		×	×	×	×	×	×	?
Parvimolge			×						×					
Lineatriton			×											
Oedipina				×	×			×	×	×	×			
Haptoglossa									×					
Eladia														×

* Occurs also in Ecuador and Bolivia.

KEY TO GENERA OF COSTA RICAN PLETHODONTIDAE

1. Tongue bolitoglossid, free all round, completely protrusible . . . 2
   Tongue attached at front and in middle, not completely protrusible . . . *Haptoglossa*
2. Costal folds 17-20, slender elongate . . . *Oedipina*
   Costal folds 14 or less, bodies not especially slender or elongate . . 3
3. Hands and feet completely webbed or palmate with only extreme tip of middle digits free . . . *Bolitoglossa*
   Hands and feet not completely webbed or palmate, one or two outer joints of most of the digits free, the tips either broad and truncate or sometimes pointed . . . 4
4. Sublingual fold absent; digits broad, usually truncate . . *Magnadigita*
   Sublingual fold present . . . 5
5. Toes grown together, the tips more or less pointed; diminutive species . . . *Parvimolge*
   Toes not grown together; webbing at base distinct; tips of digits rounded, with subterminal pads . . . *Chiropterotriton*

Genus CHIROPTEROTRITON Taylor

Chiropterotriton Taylor, Univ. Kansas Sci. Bull., vol. 30, 1944, pp. 213-218.

Type of genus: *Oedipus multidentatus* Taylor.

Two species are referred to this genus of small salamanders. Species of this genus are common in Mexico and are known in Guatemala and Honduras, but none are known in the intervening territory, thus leaving a considerable hiatus in the known distribution. Careful collecting in Nicaragua will doubtless disclose the presence of the genus in that country.

KEY TO COSTA RICAN SPECIES OF CHIROPTEROTRITON

Adpressed limbs separated by 6 costal folds; 13 costal grooves; no palatal perforation; nostril larger . . . *picadoi*
Adpressed limbs separated by 4-4¾ costal folds; 14 costal grooves, a large palatal perforation, nostril smaller . . . *abscondens*

Chiropterotriton abscondens Taylor

Text fig. 1

Chiropterotriton abscondens Taylor, Proc. Biol. Soc. Washington, vol. 61, Nov. 12, 1948, pp. 177-178 (type locality, Isla Bonita [American Cinchona Plantation] elev. 5500 ft., Volcán Poás, Costa Rica, R. C. Taylor, coll.).

Diagnosis: A diminutive *Chiropterotriton*, the adpressed limbs separated by 4 to 4½ costal folds; webbing on hands and feet involves only the basal phalanges; nostril small; an arched groove on chin and throat; 14 costal grooves; maxillary teeth 12-16 on each side in males, 19-23 in females; a median palatal perforation between choanae in adults; paravomerine teeth in a single group.

Description of the type: (R.C.T. 1414). One of the smallest species of the genus; the snout-to-end-of-vent length, 32.3 mm., tail, 37 mm. Eye large, one and one-third to one and one-half times length of snout; width of an eyelid minutely less than narrowest interorbital width; nostril small, its diameter in distance between nostrils, about eight times; a transverse groove beginning some distance behind eye crosses the throat to opposite side of head; an arched groove or line on throat and chin, the transverse groove forming its base; behind this is the curved gular fold from whose

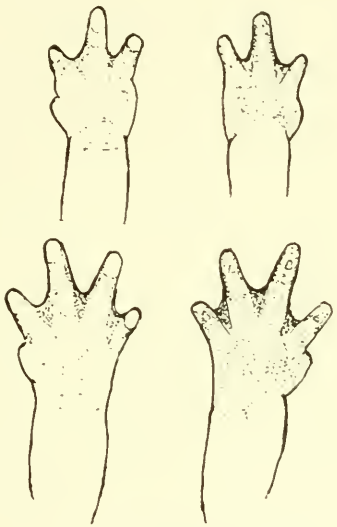

FIG. 1. *Chiropterotriton abscondens.* Type. Upper. Left hand, ventral and dorsal views. Lower. Left foot, ventral and dorsal views. (Much enlarged.)

side a lateral nuchal groove passes up on side of neck, first directed backward then forward and meets its fellow on the median nuchal line; posterior parts of eyelids not tucked under a fold; no orbitolabial groove present; a somewhat sinuous groove from eye to lateral nuchal groove; epibranchial cartilage forms a ridge or fold that extends above arm nearly to third costal groove.

Vomerine teeth 8-8, on elevated ridges beginning outside choanae, curving in and back, the two series separated by a space equal to that between two teeth, or very slightly more; paravomerine teeth forming a single patch, widened and slightly notched behind, separated from the vomerine series by a distance about equal to length

of a one row of vomerine teeth; choanae small; a median open perforation on the palate, the diameter about equal to that of a choanal opening; a free sublingual fold.

Maxillary and premaxillary teeth total 52, of which six apparently are premaxillary; vomerine teeth 8-8; mandibular teeth total 55; tongue bolitoglossoid. Swelling below nostril on edge of lip almost obsolete; 14 costal grooves, and 12 distinct costal folds, the upper edge of the folds somewhat elevated. A median, dorsal groove present; about 28 caudal grooves; cloacal walls with strongly-defined lateral folds; none or only a slight basal caudal constriction; adpressed limbs separated by 4½ to 5 costal folds.

Fingers webbed at base leaving tip of first digit, and one and a half joints of other digits free, the web between deeply excised; toes webbed at base, the tip of first digit and two joints of other digits free of web. Distinct pads under tips of digits.

Skin generally smooth, but under a lens the opening of glands give a somewhat pitted appearance; a postiliac glandular spot scarcely discernible.

Color: Above brown, with a lighter cream spot on snout in front of eyes; a pair of indefinite lighter areas on nuchal region; an indistinct row of darker flecks along the dorsolateral line, bordered above posteriorly by a lighter streak; tail brownish fawn, lighter at base, growing darker low on sides, and flecked with black; underside of body and tail and to some extent low on sides of body, uniform brown; under lens small whitish flecks present on sides of neck and below eye.

Measurements in mm.: Snout to end of vent, 32.3; tail, 37; width of head, 4.5; length of head from tip of snout to mid-ventral part of gular fold, 5.5; width of head in snout-to-vent length, 7.2; length of head in snout-to-vent length approximately 5 times; arm, 5; leg, 5.3; snout to arm insertion, 8; axilla to groin, 19.

Remarks: The curious opening in the palate, according to Mr. Irvin Baird who dissected the area, serves as the opening for a gland situated on the top of the snout and in the fontanelle opening between the processes of the premaxillary. The opening occurs in certain other species of salamanders.

The males have a somewhat larger swelling below the nostril and the cloacal opening is papillate. More details of variation in the species is given with the type description. The species is known only from the type locality in northern Costa Rica.

Chiropterotriton picadoi (Stejneger)

Spelerpes picadoi Stejneger, Proc. U. S. Nat. Mus., vol. 41, Aug. 14, 1911, pp. 285-286 (type locality, La Estrella, southeast of Cartago, Costa Rica, C. Picado, coll.); Picado, Les Broméliacées Epiphytes, 1913, p. 342, pl. 8, fig. 4.
Chiropterotriton picadoi Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 1, 1949, pp. 279, 280, 281.

Diagnosis: Legs short, failing to meet on sides by 6 mm. (length of hind leg); fingers and toes well developed, slightly webbed; vomerine teeth well separated from paravomerine tooth patch, not extending beyond choanae; 13 costal grooves; body elongate, tail cylindrical; color brown.

Description: (taken from Stejneger): Vomerine teeth in two arched, continuous series, not extending outward beyond choanae, and well separated from the paravomerine teeth, which form a single patch; head wider than body, truncate; snout short; corner of mouth under posterior edge of eye; nostrils large, rounded; body elongate, measuring four times distance from snout to gular fold, and more than three times in distance between axilla and groin; legs short, not meeting on sides by length of hind leg; fingers and toes well developed, slightly webbed; tail cylindrical, longer than head and body; skin very smooth, a distinct gular fold; 13 costal grooves. Color (in alcohol) above dark brown, with a pale irregular band extending from behind eye backward over shoulder along sides to groin, and another similar one, but fainter, from occiput on each side of back disappearing on anterior third of tail; underside paler; palms and soles still more so.

Measurements in mm.: Total length 66; snout to vent 31; tail 35; snout to gular fold 6; width of head 4; axilla to groin 20; arm 5; leg 6.

Remarks: I have examined the type specimen. The following additional characters obtain: eyelid equally as wide as interorbital distance, the eye being one and one-half times as long as snout; diameter of nostril (.3 mm.) contained in distance between nostrils (1.2 mm.) approximately four times; a distinct groove from eye to the groove crossing chin, and a groove from this to the lateral nuchal groove; tail not constricted at base; an arched groove on chin; a strong sublingual fold. Approximately 18 maxillary teeth, and at least 6 vomerine teeth in each series, the latter separated from the paravomerine teeth by a distance equal to length of one vomerine series.

The relationship of this species is, I believe, undoubtedly with the species I have described as *Chiropterotriton abscondens*. These

forms agree in having a sublingual fold and the arched groove on the chin, the large eye, approximately the same degree of development in the hand, *picadoi*, however, having the first finger somewhat more free. They likewise agree in general body characters and appearance.

The differences that appear most significant are the wide perforation of the palate in *abscondens*, the very small nostrils, probably less than one fourth of the pupil (enlarged in the very young), and the somewhat longer limbs (separated by four, very rarely nearly five costal grooves). Dunn has reported *picadoi* from La Palma, Costa Rica, and notes that the nostril is half as large as the pupil in certain specimens, and in one, a male, even a larger nostril (snout-to-vent length 25.5 mm. and not a juvenile). All juveniles presumably have large nostrils in these species. It may be that this juvenile condition is retained in *picadoi*, and lost in *abscondens*. It is also significant that the palate perforation is evident in a Harvard specimen (No. 5125) identified as *picadoi*.

The head width in snout-to-vent length in *picadoi* is 7.75 times, head length (to gular fold) in same, 5.16 times; in *abscondens* the proportions are 7.1 and 5.8, respectively.

Genus Magnadigita Taylor

Magnadigita Taylor, Univ. Kansas Sci. Bull., vol. 30, 1944, p. 218.

Type of genus: *Bolitoglossa nigroflavescens* Taylor.

Of this genus, which ranges from central Veracruz to and into South America, six forms are known to occur in Costa Rica. Three of these, *pesrubra, torresi* and *cerroensis*, are here described as new.

The relationship between *torresi* and *pesrubra*, two forms that occur at very high elevation on Cerro de la Muerte, is puzzling. *Pesrubra* extends to considerably lower elevations than *torresi*.

Key to Costa Rican Species of Magnadigita

1. Very large plump forms reaching 110 mm. snout-vent length; nearly uniform black or slate black, save for a cream ring about base of tail . . . . . *robusta*
   Medium-sized forms (less than 70 mm. snout to vent) lacking a light ring about tail 2
2. Maxillary teeth much reduced 7-9 (total 16); color nearly uniform blackish above, somewhat lighter slaty black on sides and ventral surfaces . . . . . *nigrescens*
   Maxillary teeth not greatly reduced; colors variable 3
3. Maxillary teeth total 62-78 in adults; mandibular teeth 73-97; caudal grooves 40-46. Dark colored, blackish brown to gray

brown, lighter below, often with small flecks or spots of red, rarely with an irregular stripe of buff on dorsum; costal grooves distinct ..... *subpalmata*

Maxillary teeth in adults fewer than 60; caudal grooves usually less than 30; costal grooves variable in distinctness 4

4. Legs never light or red colored, usually nearly body color; maxillary teeth 45; mandibular teeth 70; costal grooves indistinct; caudal grooves 25; brown above, not uniform; venter lavender with numerous cream flecks; throat not lighter than venter *cerroensis*

Legs usually red, yellowish or cream, rarely or never colored like body; chin and throat always lighter than venter 5

5. Larger species (67 mm. snout to vent); maxillary teeth total 50 to 57; mandibular teeth total 58 to 74; caudal grooves 25 to 31; legs bright red or pink; chin and throat reddish; dark dorsally with variable venter ..... *pesrubra*

Smaller species (54 mm. snout to vent); maxillary teeth 45; mandibular teeth 48. Dorsum gray olive, brown or blackish, uniform or with occasional light areas. Venter black, the color encroaching on sides; chin and breast unpigmented, usually cream or pinkish; costal grooves usually blackish *torresi*

Magnadigita pesrubra sp. nov.

Plate LXXVI; text fig. 2

Type: Kansas University Museum of Natural History No. 25093 ♀; Cerro de la Muerte, Costa Rica, elev. 10,900 ft.; E. H. Taylor and R. C. Taylor colls.

Paratypes: K.U.M.N.H. Nos. 25082-25092; 25094-26100, Cerro de la Muerte (where Pan-American Highway crosses) elev. 10,900 ft.; Nos. 25142-25156, Millville, western exposure of Cerro de la Muerte, 9416 ft. elev.; No. 25157 (lot of 166 specimens, from 9416 to 10,900 ft. elevation, Cerro de la Muerte; R.C.T. Nos. 3583 [lot number for 128 specimens]), 9416-10,900 ft., Cerro de la Muerte.

Diagnosis: A moderately large form reaching a snout-to-vent length of 67 mm.; tail 64 mm.; tongue bolitoglossid; no sublingual fold; paravomerine teeth in a single patch; 13 costal grooves (counting one in axilla); limbs when adpressed separated by two and one-half costal folds; tail somewhat constricted at base; 28 + caudal grooves; digits with webs, the web including inner finger and toe; the other digits having from one and one-half to two phalanges free; limbs pink or red; a pinkish area on side of neck and head involving also chin and part of breast; dorsum and sides blackish or blackish brown; ventral surface slate black or brownish black.

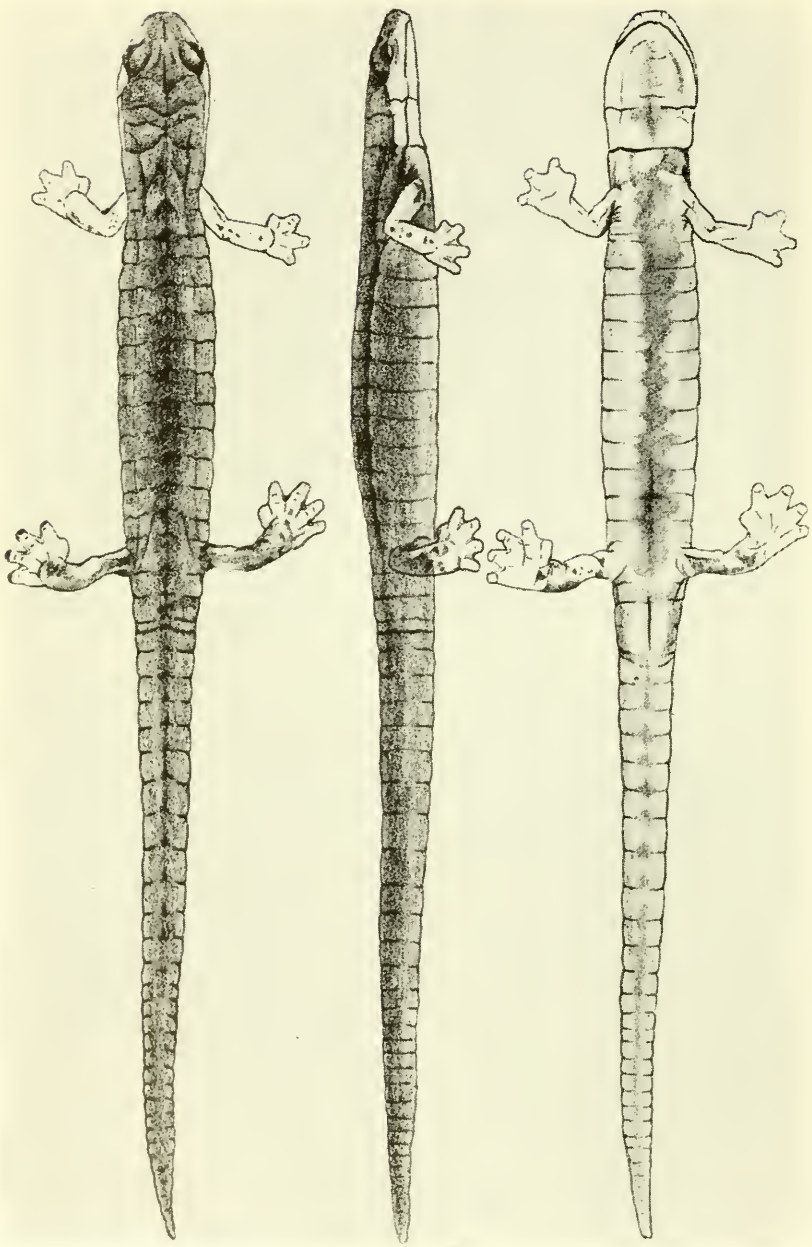

PLATE LXXVI. *Magnadigita pesrubra* sp. nov. Type, K.U.M.N.H. No. 25093. Total length, 128 mm.

Description of type: Head rather flattened, the eyes relatively small, their length distinctly less than length of the snout; no canthus; nostril nearly terminal; a small subnarial swelling below nostril (larger in males); more or less distinct groove borders inner edge of orbit; width of an eyelid (1.8) in interorbital interval (4 mm.) a little more than two times; a groove from side of head crosses in front of jaw angle, and passes across the chin; a distinct gular fold passing straight across the neck and reaching up somewhat on side of neck; from this emerges the lateral nuchal groove which passes vertically some distance then runs diagonally forward to meet its

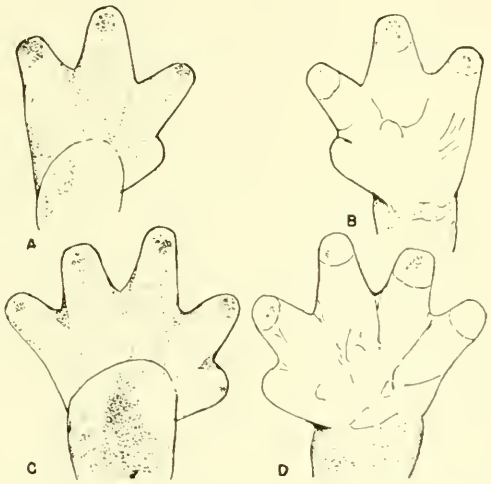

FIG. 2. *Magnadigita pesrubra.* Type. A. Left hand, dorsal view; B. Left hand, ventral view; C. Left foot, dorsal view; D. Left foot, ventral view. (Much enlarged.)

fellow on middorsal line; (males with a small submental hedonic gland); posterior ends of eyelids tucked under a short diagonal fold; a deep groove from eye curves down to touch the beginning of the groove that crosses chin then runs back to touch the beginning of the lateral nuchal groove, the whole line forming an angle.

Choanae small, with a narrow emergent groove; vomerine teeth on two elongate curving ridges beginning beyond outer level of choanae, curving back slightly but failing to meet on the median line by a distance equal to greatest diameter of a choana; about 12 teeth on each side; paravomerine teeth in single large patch 6 mm. long, its greatest width 4.5 mm. posteriorly, the least width anteriorly

1.8 mm.; the number of mandibular teeth 28-28; premaxillary teeth 3.

Adpressed limbs separated by two and one-half folds; webbing on hand leaves only inner tip of first finger free; other toes with two phalanges free (or slightly more) the web however forming a fringe so that free part of toes are wider at base than tip; inner toe with only tip free; other toes with one and one-half to two phalanges free, the web slightly excised. Body subcylindrical, the tail slightly compressed, higher than wide; thirteen costal folds (counting one in axilla), and well defined on venter to mid-ventral line; a distinguishable longitudinal depression above the costal folds; surface of the latter longitudinally wrinkled. Tail constricted at base; about 28 caudal grooves, and a small portion of the tail (12 mm.) in which the grooves cannot be discerned; tail approximately as long as head and body.

Color in life: Above dark lead to brownish black; arms pink to red; hind feet somewhat orange-pink with some pigmentation on the thigh and tibia; a faint lighter spot on glandular area behind insertion of hind limb; chin and throat to gular fold, immaculate pink, the color becoming somewhat more reddish on side of neck below the postorbital groove and on the side of the head; venter dull gray or brownish slate, lighter than on dorsum, with an occasional pinkish fleck; tail slate, scarcely lighter on its ventral surface.

Measurements in mm.: Snout to end of vent, 67.2; snout to foreleg, 17.3; axilla to groin, 37; tail, 66; width of head, 9.5; length of head to gular fold, 16; width of body, 10.4; arm, 15.2; leg, 15.2; head width in snout-to-vent length, 7.05 times; head to gular fold in same, 4 times.

Variation: The pink or red coloration of chin, throat, arms and legs is, I think, invariably present; however there may be some darker pigmentation present on the limbs. Rarely there may be very little pigment also on digits but these are more frequently without any pigment. Occasional specimens may have the venter somewhat brownish, in which case the brown may be more or less evident on sides of dorsum. Occasional specimens have the pink color replaced in part with orange, especially on the side of the head.

Remarks: In the forested areas where *pesrubra* was taken, specimens were encountered about logs and in piles of trash and leaves. Many of the females have large yellow ovarian eggs, and a few egg masses were found in leaves with the female coiled about them.

MEASUREMENTS AND DATA ON MAGNADIGITA PESRUBRA

No. (field)	3583	3577	3589	3536	3575	3578	3553	3534	3540	3558
Sex	♀	♀	♀	♀	♀	♂	♂	♂	♀	♂
Snout to vent	67	66	62.2	62	60.5	57	56	55	54.5	54
Snout to foreleg	17	16.5	17.6	17.3	16	17	17	16	15.5	16
Axilla to groin	37	36	35	33.6	34	29.5	29.2	29	29.6	28
Tail	63	65	36+	62	60	59	59	57.2	52	57
Arm	14.6	14	13	12.3	14	13	13	13.2	11.6	13
Leg	15.8	15.2	14	14.3	14.1	14	14	13	12	13
Head width	9.2	9.2	8.7	9	8.8	8.8	9	9	8.9	9
Head length (gular fold)	13.5	14	13.7	14	12.3	13	13	13	12.1	12.7
Head width in snout to vent length	7.28	7.14	7.15	6.9	6.87	6.46	6.22	6.11	6.18	6.0
Head to gular fold in same	4.96	4.70	4.54	4.43	4.91	4.39	4.30	4.23	4.20	4.25
Costal grooves	13	13	13	13	13	13	13	13	13	13
Caudal grooves	28+	31+	25+	26+	30+	29+	30+	31+	31+	30+
Maxillary teeth (total)	57	54	55	50	54	55	52	54	54	54
Premaxillary teeth	4+	4	5	4	5	3	3	5	5	5
Prevomerine teeth	33	27	25	21	29	25	23	26	31	29
Paravomerine teeth	174	170	106	131	120	138	144	148	140	120
Mandibular teeth	74	72	67	59	67	68	74	74	58	67

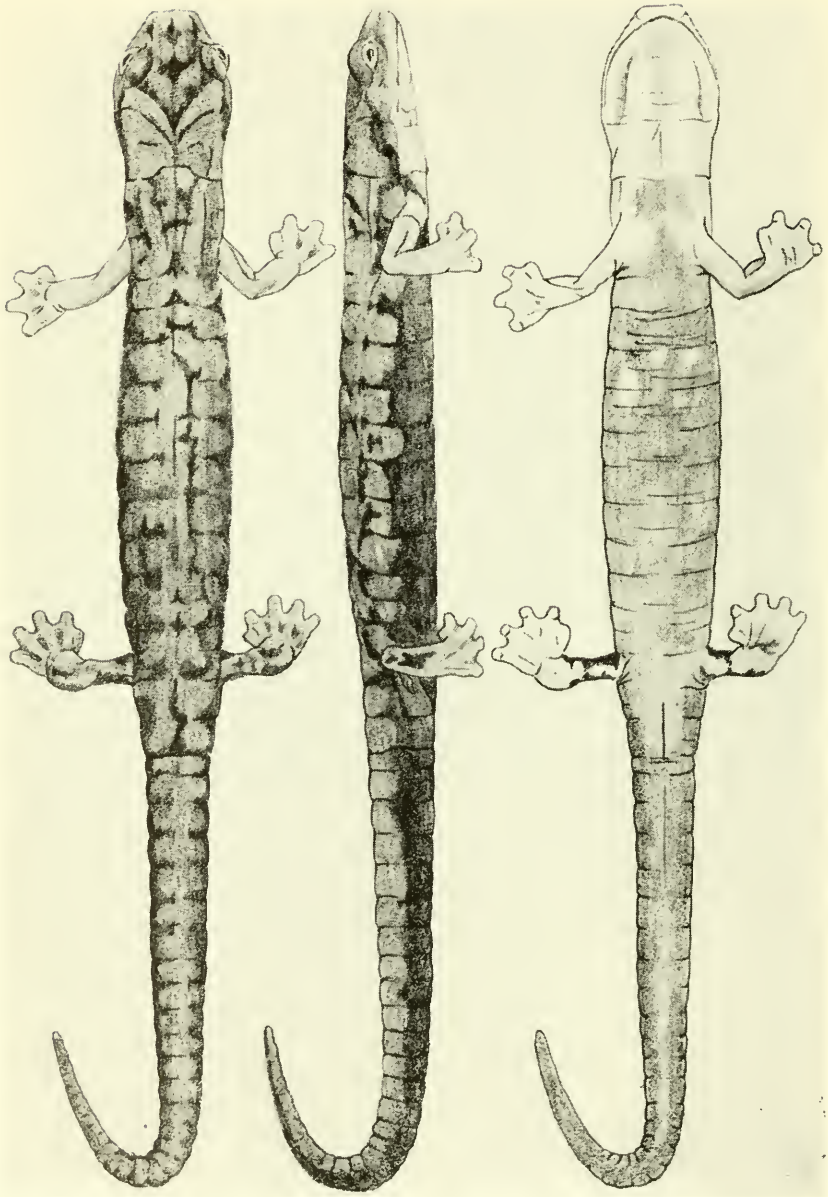

PLATE LXXVII. *Maguadigita torresi* sp. nov. Type, K.U.M.N.H. 25104. Total length, 111 mm.

Magnadigita torresi sp. nov.

Plate LXXVII

Type: Kansas University Museum of Natural History No. 25104 ♂, Summit of Cerro de la Muerte, Costa Rica (where Pan-American Highway crosses) 10,900 ft. elev., Aug. 17, 1947; R. C. Taylor and E. H. Taylor collectors.

Paratypes: K.U.M.N.H. Nos. 25101-25103; 25105-25116; 25116A (lot number for 30 specimens); R.C.T. No. 3485 (lot number for 42 paratypes). All topotypes.

Diagnosis: A medium-sized salamander reaching a known snout-to-vent length of 54 mm.; tail 55 mm.; the width of head in snout-to-vent length 5.8 times; adpressed limbs separated by two costal folds; tongue bolitoglossid; no sublingual fold; paravomerine teeth in a single patch; tail constricted at base; 13 costal, 29 + caudal grooves; usually brown more or less flecked or clouded with black; venter slate-black or black with lighter spots; chin and breast not pigmented; the side of head and neck usually more or less pigmented, but less so than top of head; usually an irregular dark mark from eye to arm; digits truncate at tips.

Description of type: A medium-sized species, the head not broader than the body, its width in snout-vent length 5.8 times; eye of moderate size, the width of an eyelid (2 mm.) much narrower than the narrowest interorbital distance (2.8 mm.); top of head flat, but curving slightly forward; snout moderately high, sharply truncate; subnarial swellings prominent; a groove begins behind eye, runs somewhat diagonally back to where it bisects a groove that crosses jaw angle and chin, but does not reach back to the nuchal groove; a strong gular fold passing nearly straight across neck; at its terminus the nuchal groove arises, passes slightly forward and upward to dorsal level of body and can be traced to the median line; the posterior corners of eyelids end at a short groove, but there is no diagonal fold present; maxillary teeth 22-23; the premaxillary teeth five, piercing the gum; vomerine teeth in two short rows of 12 teeth each, the rows beginning beyond outer level of choanae, curve in and strongly back, but are separated mesially by a distance a little less than width of a choanae and from the paravomerine teeth by an equal distance; paravomerine teeth in a single group bearing approximately 132 teeth; mandibular teeth approximately 24-24; no sublingual fold; 13 costal grooves counting one in groin, the last two costal folds only partially separated, the groove not descending to lower level of body; 29 caudal grooves,

usually distinct across ventral surfaces and reaching high on sides; cross section of the body subtriangular rather than subcylindrical; the tail is subcylindrical. Skin showing rather indistinct pitting, the sides with fine corrugation; a postiliac glandular spot.

Arm moderately long, fingers webbed, the first largely involved in web with only a rounded tip free; other toes with two phalanges free, their sides subparallel; inner toe almost completely involved in web, the three middle with approximately two free phalanges, the outer with little more than one phalanx free; all of the digits save two inner with a small subterminal pad; cloacal walls papillate (female with diagonal folds).

Color: Above, dull olive-brown clouded and flecked with blackish, and many of the costal grooves blackish; venter slate-black with a few small light flecks, the dark color reaching up a short distance on the sides. Chin, cream or pinkish; sides of head and snout lighter than top of head, but usually pigmented except on upper lip; an indistinct dark line from eye to arm, below which the color is much lighter; arm light brown lightly pigmented save on under surface which may have areas without pigment; breast lighter, somewhat clouded with darker (the clouding more frequently absent). Tail brownish above, clouded and flecked with black, the sides and ventral parts slate-black.

Measurements in mm.: Snout to end of vent 55; tail 56; snout to foreleg 16; axilla to groin 30, width of head 8; snout to gular fold 12.8; arm 10.8; leg 13.

Variation: This species and *pesrubra* occupy the same identical habitats on the summit of Cerro de la Muerte, occasionally both forms being taken under the same rock or mass of moss. Adults of the two forms may usually be readily differentiated; however, the young of the two species are somewhat difficult to separate. The reason for this is the very considerable variation in color and markings of both species. The most common dorsal markings of *torresi* are a brown dorsum, the sides brownish to an irregular line a little below midway, then the remainder of side black, with a blackish venter. Occasionally the brown of the body extends on to the tail a greater or lesser distance. Only rarely however is the brown uniform; it may be flecked or clouded with dusky; the head may be darker than body, blackish, with flecks of brown, or brownish flecked with black. The limbs are lighter than dorsal color and may sometimes be pinkish. The sides of neck and of head are usually pigmented like the top of the head, or they may be

lighter. The chin and breast, however, are light flesh, occasionally with a pinkish reflection or wash. The abdominal region is often spotted with from two to five large lighter spots, irregularly disposed.

There are two characters that differentiate this species: the smaller size, and the characteristic of the hands and feet. Thus the emarginations between the digits are V-shaped in *pesrubra* and more nearly U-shaped in *torresi*. This is due to the fact that the webbing between the fingers and toes of *pesrubra* tends to form a fringe of diminishing width and extends farther out than the depth of the emargination. The shape of the free parts of the digits are thus somewhat triangular, their tips more rounding, less truncate. In *torresi* the toes are somewhat more truncate and the web extends but little beyond the level of the emargination between the digits. Thus the free part of the digits themselves have their sides more nearly parallel and are more nearly quadrangular than triangular.

Remarks: This species was found to be especially common under rocks, in moss about bamboo clumps, in fact almost anywhere that cover could be found. There is no forest, but there are extensive thickets, of a dwarf bamboo that reaches a height of *circa* ten feet. There are other shrubs, a few boulders and scattered rock. The place is subject to sudden changes of temperature and ice is said to be not uncommon. On one day (Aug. 17) we were collecting there when the temperature dropped rather suddenly to near 40 degrees F. With wind and rain falling through a heavy fog, we were soaked and prevented from finding familiar territory for several very miserable hours. Numerous travelers coming up from the hot coastal lowland to cross over the mountain-pass to the opposite side are said to have lost their lives here on this summit because of the cold. Thus the name, Cerro de la Muerte, the mountain of death.

Magnadigita subpalmata (Boulenger)

Plates LXXVIII, LXXIX

Spelerpes subpalmatus Boulenger, Ann. Mag. Nat. Hist., ser. 6, vol. 18, 1896, pp. 341-342 (type locality, La Palma, Costa Rica; collected by C. F. Underwood); Proc. Zool. Soc. London, June 7, 1898, p. 478; Günther, Biologia Centrali-Americana; Reptilia and Batrachia, Dec. 1901, pp. 300-301.

Oedipus subpalmatus Dunn, Field Mus. Nat. Hist., Zool. Ser., 1924, vol. 12, pp. 99, 100; The Plethodontidae, Smith College Publ., 1926, Northampton, Mass., pp. 390-393 (Costa Rican localities given are Rancho Redondo, Turrialba, Barba and Irazú [volcanoes], Cot, Poás [volcano], Tablaze [?], Cerro de la Muerte).

? *Oedipus morio* Cope, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 8, p. 96; Proc. Amer. Philos. Soc., vol. 18, p. 271.

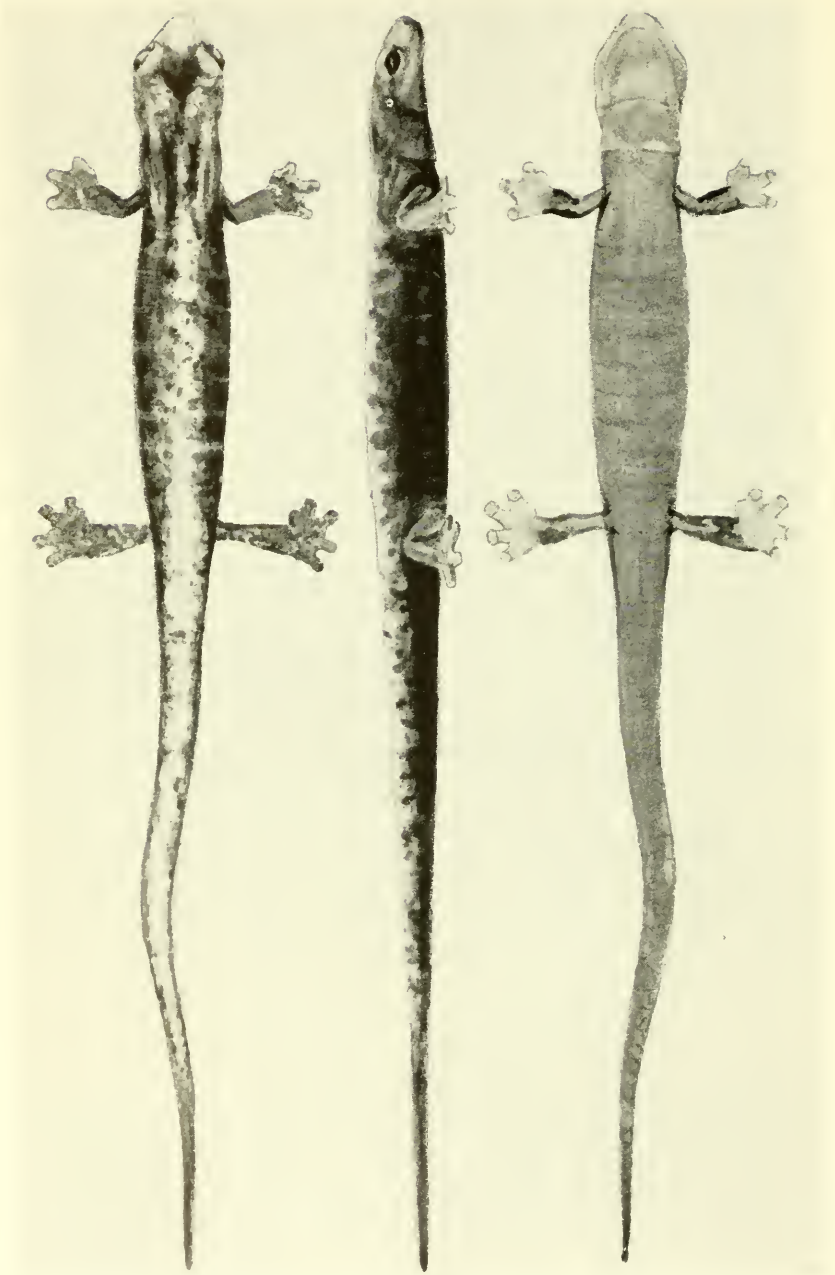

PLATE LXXVIII. *Magnadigita subpalmata* Boulenger. Color variant. R.C.T. No. 3131, Isla Bonita, eastern drainage, Volcán Poás, Costa Rica. Total length, 127 mm.

Magnadigita subpalmata Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, May 15, 1944, p. 218 (referred to *Magnadigita*); *idem*, vol. 33, pt. 1, April 20, 1949, pp. 279, 280, 281 (occurrence in Costa Rica).

Diagnosis: Medium-sized species, reaching 60 mm. in snout-to-vent length; maxillary teeth in adults total 62 to 78; mandibular teeth 73 to 97; dorsum dark lavender brown, blackish brown or grayish black, rarely speckled with red or with a buff line; venter uniform blackish or blackish brown, lighter than the dorsum; caudal grooves 40-45.

Description of species: (K.U.M.N.H. No. 28124 ♂). Head but little broader than body (except gravid females with body distinctly wider); width of upper eyelid (2.8 mm.), in interorbital distance (3.6 mm.) about 1.3 times; snout truncate, curving very slightly when seen from above; prominent swellings below nostril; a large hedonic gland on chin; eye longer than snout; a strong groove from behind eye runs back and down, continuous with a groove that crosses back of jaw and surface of throat; a gular fold, passing nearly straight across neck; nuchal grooves arising on each side of fold continuous to middorsal line; a secondary vertical groove more or less evident between the nuchal groove and that crossing back part of jaw; occiput, interorbital and preorbital areas with small pits, the skin thickened with small depressions tending to form a reticulum; a slightly depressed groove follows outline of upper eyelid; nostril small; palate in front of prevomers vaulted, with a minute medial opening; choanae small, the diameter of one (.25 mm.), contained in the distance between the two (2.2 mm.) six times; maxillary teeth 38-37; vomerine teeth, 12-12, on two elevated ridges becoming lower mesially; paravomerine teeth about 170 in single patch with a slight toothless line mesially; mandibular teeth about 42-42. Arm short, its length in snout-vent length 4.2 times; leg in same distance, 3.9 times; fingers broad truncate, the outer webbed at base, the first almost wholly involved; the three outer free for two to two and one-half phalanges; four outer toes likewise free for about same distance; adpressed limbs separated by one and one-half to two costal folds; 13 costal grooves and 12 costal folds, the posterior groove somewhat in front of limb insertion; tail longer than head and body, cylindrical, constricted a little at base; 44 caudal grooves; a distinct longitudinal, lateral groove above thickened part of costal folds; a postiliac gland (behind insertion of leg).

Color: General color slate-gray with brownish flecking evident over back; sides slightly lighter in tone than back; chin dirty gray-

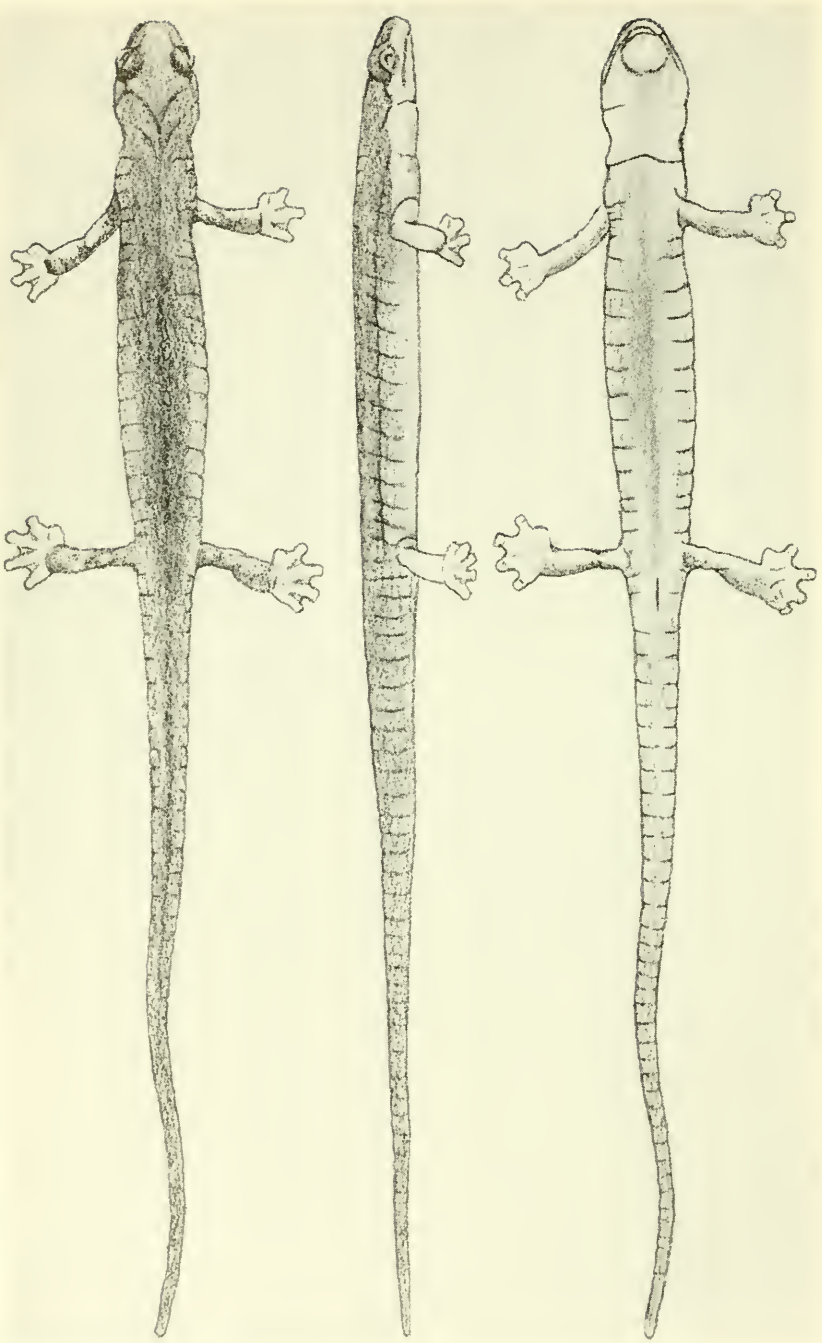

PLATE LXXIX. *Magnadigita subpalmata* Boulenger. Typical. K.U.M.N.H. No. 28124, Isla Bonita, eastern drainage Volcán Poás, Costa Rica. Actual size.

cream as are under surfaces of hands and feet, and to a lesser extent, arms and legs; venter grayish, the median area darker than outer portions; tail dark above flecked with brown; below almost uniformly dark; a few lighter flecks near base of tail and on under surface of legs.

Variation: The color of *Magnadigita subpalmata* varies considerably. Boulenger calls attention to it in the type description.

In the large series at hand there are two general types of coloration.

1. Gray black on dorsal and lateral surfaces of head, body and tail; or blackish with indistinct clouding or indefinite flecks of brown, or reddish brown. In these specimens the ventral surface is often uniform brownish black, or leaden with a few scattered cream flecks. Occasionally in this form the brown is united to form fawn or reddish cream spots, or rarely a broad median stripe with irregular edges that may extend to the tip of the tail.
2. Uniformly grayish black above with lighter venter of a dirty grayish flesh-color, that extends up to near the middle of the sides. In these specimens the costal folds appear as darker lines on the lighter coloring. These specimens when placed under water show a very slight brownish mottling but seemingly none of them have the whitish ventral flecks.

Females generally have a broader head and body than males of the same snout-vent length. The number of caudal vertebrae is normally between 40-45 in all adults, the tip being less differentiated in some of the specimens than in others. The tooth-count shows an increase in teeth for increase in body length. The maxillary tooth-count for the largest specimens (57.5 to 58.6 mm. snout-vent length) is between 37 and 40 on each side; premaxillary teeth in females are six or eight; in males they pierce the lip and are usually five in number. They are sometimes lost and sometimes the missing tooth may be found deep in the lip tissue. The prevomerine teeth in this size group vary between 13 and 17, the teeth beginning considerably outside the outer level of the choanae. The expected number of paravomerine teeth for this group seems to vary considerably, the average being about 170. The mandibular teeth on each side number between 42 and 50. The number of teeth present reduces rapidly as younger, smaller specimens are counted.

The length of the free part of the fingers was greatest in a specimen taken in a bromelia at Cervantes, and some slight differences in the size of the hand and foot were noted in the other populations.

TABLE OF DATA AND MEASUREMENTS OF MAGNADIGITA SUBPALMATA

COLLECTION	RCT	RCT	RCT	KUMNH	KUMNH	KUMNH	KUMNH	KUMNH	RCT
Number	3131	2104	3136	28108	28119	28124	28107	28126	3134
Sex	♀	♀	♀	♀	♀	♂	♂	♂	♂
Snout to vent	58	58	58.6	57.5	51	55.5	55.5	53.5	53
Snout to foreleg	18	15	18	15.5	15	15.3	15	14.5	14.5
Axilla to groin	31.5	34	31	32	28	30	30.5	29	30
Tail	71	75	61	lost	56	75	72	72	72
Arm	12	11.8	11	11.6	11.8	13	12	12	12
Leg	12.8	13	12	12	12	14	12	13	12
Head width	8.8	8.8	9	9	9	8.8	8.8	7.9	7.6
Head length	14	12.2	13	13	12.2	12.2	12	11.6	12
Head width in body length	6.59	6.59	6.5	6.4	5.7	6	6	7.6	7
Head length in body length	3.9	4.8	4.5	4.4	4.18	4.55	4.6	4.6	4.4
Costal grooves	12	13	13	13	13	13	13	13	13
Maxillary teeth	37–38	40–38	36–39	33–36	28–29	38–37	29–33	30–32	35–35
Premaxillary teeth	6	6	7	8	5	4	5	5	3+
Prevomerine teeth	13–15	17–17	16–14	14–15	12–14	12–12	11–12	15–15	12–14
Paravomerine teeth	174	194	155	168	152	171	148	182	176
Mandibular teeth	49–48	48–44	45–50	42–42	42–42	42–42	36–38	35–38	43–44

Specimens from high on Volcán Irazú are seemingly somewhat dwarfed.

Remarks: Specimens were taken at the following localities: Volcán Irazú, 8500 ft. elevation (six specimens in bromelias); Volcán Irazú "Roberts Hotel 7000 ft.", one specimen collected by Prof. Rubén Torres Rojas; Cervantes, south slope of Volcán Irazú, 5000 ft. elevation in bromelia; Isla Bonita (American Cinchona Plantation); Volcán Poás, 5600 to 6500 ft., 43 specimens. This latter group of specimens were found on the ground at night moving over the surfaces where road-cuts left more or less vertical surfaces with a meagre growth of small plants or mosses. Specimens were taken here only at night. The land had recently been cleared of forest and no bromelias were available at the immediate places where the specimens were taken. No examples were found in the daytime, nor were their daytime hiding places determined.

The tail has a slight constriction at its base but the tails are not especially fragile, since only two or three of this large series have lost their tails. This, in part, may be a result of their quietness when picked up.

The Cervantes specimen has distinctly longer and slenderer fingers.

Magnadigita nigrescens Taylor

Plate LXXIXA; text fig. 3

Magnadigita nigrescens Taylor, Univ. Kansas Sci. Bull., vol. 33, part 1, Apr. 20, 1949, pp. 282-283 (type locality, Boquete Road Camp, on Pan-American Highway, between Millville and San Isidro El General, Costa Rica; elevation 6000 ft., E. H. Taylor coll.).

Diagnosis: Uniformly blackish above, slaty black on sides and ventral surfaces; hand and foot webbed, the terminal joint of truncate digits free of web except that of inner digits; thirteen costal grooves; nostril small; paravomerine teeth in a single patch, notched behind; 11-11 vomerine teeth, each series arranged partly in two series, beginning outside level of choanae, the two groups separated by twice the diameter of a choana; no sublingual fold; maxillary teeth reduced, 7-9.

Description of the type: (K.U.M.N.H. No. 23816; field No. 914.) Adult ♀; head broad, the snout bluntly rounded, somewhat truncate; a slight swelling on lip below nostril; eye moderate, its diameter longer than snout; posterior part of eyelids fit under a diagonal fold; a strong gular fold on neck with a nuchal groove arising from each side, which meets its fellow on the middorsal line of the neck; anterior to gular fold, a groove completely crosses

chin and ascends either side of head, crossing near angle of mouth and terminating at the postorbital groove; latter arises at eye, and extends back but does not reach nuchal groove; thirteen costal grooves counting those in axilla and groin; adpressed limbs sepa-

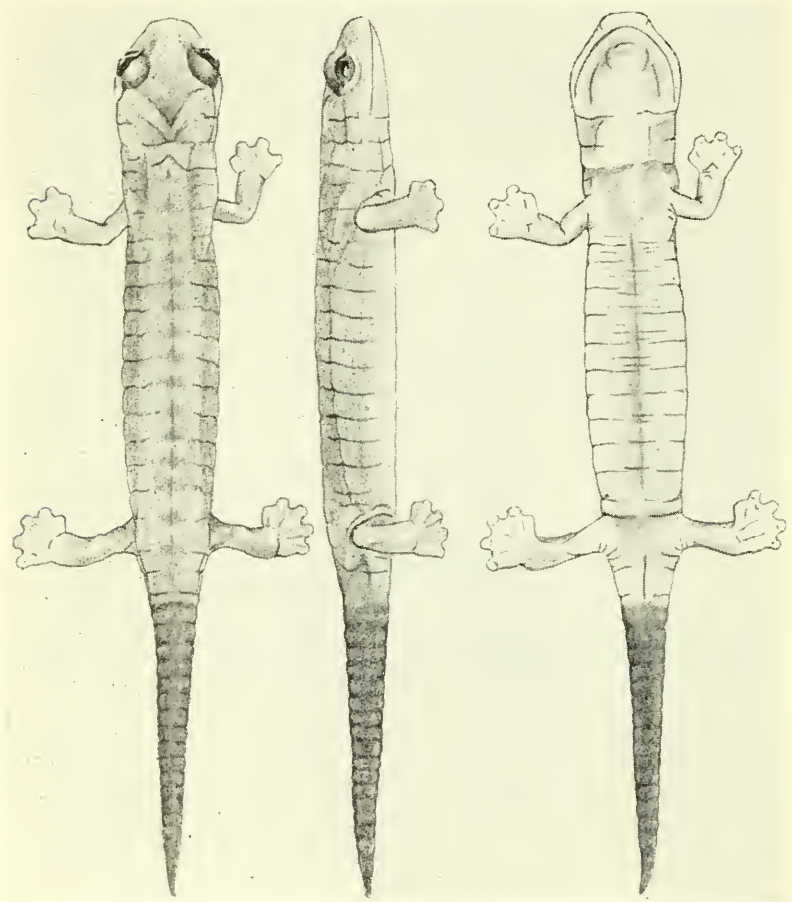

PLATE LXXIXA. *Magnadigita nigrescens* Taylor. Type K.U.M.N.H. No. 23816, Boquete Camp between Millville and San Isidro El General, elev. 6000 ft., Costa Rica. Total length, 70 mm.

rated by between two and one-half to three costal folds; fold resulting from the posterior extension of the epibranchial cartilage reaches second costal fold; tail regenerating; presumably a basal constriction on tail; walls of cloaca with smooth folds; glandular area behind insertion of leg not especially distinct.

Skin generally smooth, but area on snout and interorbital region somewhat rough; venter crossed by very numerous fine striations.

Limbs rather short, the broad digits united by a web, almost palmate; the terminal joint of the digits, other than the inner, subtruncate, with terminal joint free, and small subterminal pads present below tips of digits; between toes the web may be slightly excised.

Floor of mouth without a sublingual fold; choanae very small, their diameter contained in distance between them about six times;

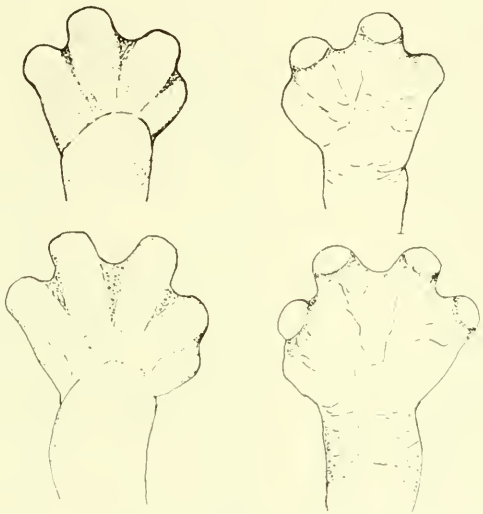

FIG. 3. *Magnadigita nigrescens*. Type. Upper. Left hand, dorsal and ventral views. Lower. Left foot, dorsal and ventral views. (Much enlarged.)

paravomerine teeth in a single elongate patch widening gradually posteriorly and notched behind, anteriorly narrow and, save for two or three scattered teeth, widely separated from the vomerine teeth; the vomerine series of about eleven teeth each begin beyond the outer level of the choanae and curve back, separated from each other by a distance equal to twice diameter of choana; each series arranged partially in two rows; maxillary teeth small, 7-9 almost covered by gums; only a single premaxillary tooth present; 25 mandibular teeth on each side of jaw.

The tail (regenerated) is shorter than head and body, with eighteen caudal grooves discernible; width of head in head-body length, 5.2 times; length of head to gular fold (lateral) in head-body length, 3.9 times.

Color: In life nearly uniform slate-black above and below; in preserved state the dorsal color is dark brown, the sides slate-black, the venter blackish brown; under side of limbs lighter brown; under side of hands and feet grayish white; chin lighter brown than venter.

Measurements in mm.: Total length (tail regenerated), 70; snout to arm, 15; snout to end of vent, 46; axilla to groin, 25; arm, 9.8; leg, 10.1; head width, 8.8; head length to gular fold (lateral), 11.8; head length to gular fold (median), 11.1.

Remarks: Only a single specimen of this species was taken. It was obtained from within the naturally-hollow stalk of a large-leafed plant. The entrance had been gained through a hole bored by an insect. It was found nearly a meter below the point of entrance when the stalk was accidentally split.

The great reduction of the maxillary teeth occurs in no other Costa Rican species of the genus that I have examined, and I am uncertain as to its closest relationship.

Magnadigita cerroensis sp. nov.

Plate LXXX

Type: University of Kansas Museum of Natural History No. 29961, collected on Cerro de la Muerte at approximately 7000 feet elevation, Pacific slope, 2 km. below Millville on the Pan-American Highway, August 15, 1947; R. C. Taylor and E. H. Taylor collectors.

Diagnosis: Light brown on body and limbs; venter, chin and part of underside of tail lavender-brown with numerous cream flecks. Tail darker, approaching blackish at the dorsal tip; shorter than snout-vent length; snout high, rather narrowed but truncate; 13 costal grooves, scarcely discernible; adpressed limbs separated by two costal folds; maxillary tooth series reduced, 22-23; mandibular teeth 34-36; paravomerine teeth 141; tongue free without trace of a sublingual fold.

Description of type: A medium-large species of the genus; head distinctly wider than the body; the snout short, constricted or narrowed in front of eyes, relatively thick; length of eye (length of eyelid) slightly less than length of snout; width of upper eyelid in interorbital distance, 1.8 times; tip of snout rather truncate (actually with a very slight convexity seen from above); subnarial swellings moderate; nostrils small; sides of snout with a very slight slope to edge of lip; the canthus rounding; a groove or depression from behind eye, bends down and back to connect with the transverse

PLATE LXXX. *Magnadigita cerroensis* sp. nov. Type. K.U.M.N.H. No. 29961. Cerro de la Muerte, 7000 ft. elevation on highway about 2 km. below Millville, Costa Rica. Total length, 114.5 mm.

groove that crosses the jaws and curves slightly forward across the throat; a well-defined, nearly-straight gular fold passes across the neck; nuchal grooves arising from the edges of the gular fold indistinct, not reaching the middorsal line; posterior extension of epibranchial cartilage extends above arm, forming a fold reaching to near the third costal groove; anterior part of palate moderately arched, with a minute groove or perforation; choanae oval, the greatest diameter of one in distance between choanae, about 3.5 times (choana on right side somewhat deformed).

Maxillary teeth 22-23 (counting missing teeth), small; teeth on prevomers 11-12, in elevated series separated mesially by a distance equal to that between three teeth, separated from the paravomerine teeth by a somewhat greater distance; paravomerine teeth total about 140, in a single series, the length, 5.5 mm., a little less than twice the width (3 mm.); mandibular teeth 34-36, relatively small. The premaxillary teeth 3 (possibly 5 normally), somewhat larger than the maxillary series; tongue free, no trace of a sublingual fold.

Arms and legs strong, separated, when adpressed, by approximately two costal folds; hand webbed with first finger completely in web, second with one joint, the two outer with one and one-half joints free; the webbing somewhat emarginate between digits; the sides of the fingers not parallel or emarginate; three outer toes with one and one-half phalanges free, the second with one, the inner completely enclosed with web; adpressed limbs separated by approximately two costal folds; tail shorter than snout-vent length, slender, cylindrical; the caudal grooves not clearly discernible but approximately 27 grooves (vertebrae); tail slightly constricted at base. Cloaca with strong, chiefly longitudinal, folds; a postiliac gland in evidence, lighter in color than surroundings; approximately 13 costal grooves and 12 folds (there is some doubt that this is the actual count, since the grooves are poorly defined).

Measurements of type in mm.: Total length, 114.5; snout to vent, 62; snout to forearm, 16; axilla to groin, 32.6; tail, 52.5; width of head, 9; head length, 13.6; arm, 13.5; leg, 14.3; head width in snout-vent length, 6.8 times; head length in snout-vent length, 4.56 times.

Color: Above the basic color is cream with brownish stippling and streaking, giving a general brownish coloration; posteriorly the streaks are longitudinal; sides a little darker than back; lavender brown on chin, venter and underside of tail, with numerous cream markings; underside of limbs mottled brown and cream; tail above darker; upper eyelid blackish.

Remarks: The species occurs in the same locality where *Magnadigita pesrubra* is the common species, but the latter may readily be distinguished by the reddish limbs and chin, the distinctness of the costal grooves, and the longer tail having 34-36 caudal grooves (vertebrae), (the estimated number for *cerroensis* being 27).

From *Magnadigita nigrescens*, it differs chiefly in dental and foot characters, *nigrescens* having only the terminal phalanges of the three outer fingers and toes free, and the dentition reduced—the maxillary teeth being 7-9, instead of 22-23 in equal sized specimens of *cerroensis*. (The tail in the type of *nigrescens* has been reproduced.)

The head is distinctly wider than that in *pesrubra* of equal snout-vent length and the color is different. It differs from *subpalmata* in the shorter tail (tail practically equal to snout-vent length in *subpalmata*), different coloration, a smaller series of maxillary teeth, 22-23 (36-40 in largest *subpalmata*), smaller mandibular series, 34-36 (44-50 in *subpalmata*), fewer caudal grooves, 34-35 (compared with 42-44 in *subpalmata*). Differences of size and color markings between this form and *robusta* are such as to distinguish the two readily.

Magnadigita robusta (Cope)

Plate LXXXI

Oedipus robustus Cope, Proc. Acad. Nat. Sci. Philadelphia, 1894, pp. 194-195 (type locality "Faldas of Volcano Irazu" from J. P. Cooper, No. 226 [now AMNH 5464]); Dunn, Field Mus. Nat. Hist., Zool. Ser., vol. 12, no. 7, May 19, 1924, pp. 99, 100 (key); The Plethodontidae, Smith College Publ., Northampton, Mass., 1926, pp. 362-364, 439.

Spelerpes bocourti Boulenger, Proc. Zool. Soc. London, 1898, p. 478 (listing only), (*nec.* Brocchi, Étude sur les Batraciens; Miss. Sci. Mexique . . . livr. 3, 1883, pp. 111-112, pl. 18, f. 2); Günther, Biologia Centrali-Americana; Reptilia and Batrachia, Jan. 1902, p. 301, pl. 76, fig. A (*nec.* Brocchi, *loc. cit.* Günther gives a figure of a specimen from La Palma, Costa Rica; lists specimens from La Palma, 1600 meters, and Cariblanco collected by Biolly and C. F. Underwood).

Magnadigita robusta Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, May 15, 1944, p. 218 (*robusta* referred to the genus *Magnadigita*); *idem*, vol. 33, pt. 1, Apr. 20, 1949, pp. 279, 280, 281.

Diagnosis: This species, the largest salamander known in Costa Rica, may readily be distinguished from other Costa Rican salamanders by its black color, more or less uniform over the entire surface save for a whitish or cream ring around the base of the tail, and some reddish brown or gray flecking on the tail and limbs; maximum size, 110 mm.

Description of species: From K.U.M.N.H. No. 25071, Isla Bonita, Volcán Poás. The head (18 mm.) broad, the outline slightly

angular, reaching its greatest width immediately behind eyes; the neck strongly narrowed, its width 14 mm.; gular fold curving forward very slightly on neck; nuchal grooves more or less distinct to median dorsal line; snout short; length of eye at least a fifth longer

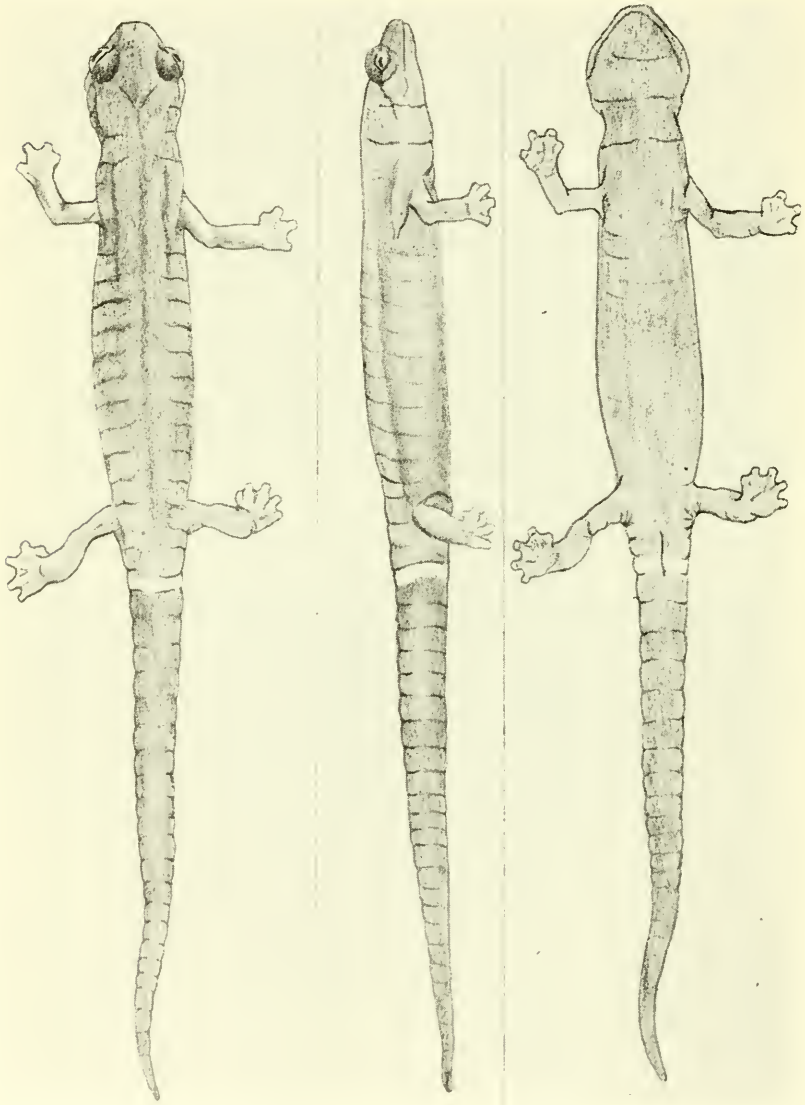

PLATE LXXXI. *Magnadigita robusta* (Cope). K.U.M.N.H. No. 25071. Isla Bonita, eastern slope Volcán Poás, Costa Rica. Total length, 209 mm.

than snout, and equal to distance from eye to middle of tip of snout; tip distinctly truncate, canthal region rounding; under a lens, minute pits on dorsal surface of head visible; interorbital area somewhat corrugated; a groove arising on side of head passes across throat curving forward slightly on ventral surface (in some of the specimens this groove cannot be traced across the throat); a distinct postorbital groove curving back and down from eye, crossing head groove but not reaching as far as the lateral nuchal groove; lateral extension of epibranchial cartilage above arm forms an elevated fold to second costal groove; tongue free, without trace of a sublingual fold; choanae small, the diameter of one in distance between them, five times.

Maxillary teeth 51-53, relatively small, the series separated from premaxillary series by a narrow hiatus; vomerine teeth 20-21, in two elevated series beginning beyond outer level of choanae, the series curving slightly forward then back slightly, mesially separated from each other by a space equal to that between two teeth; paravomerine teeth seemingly in a single group (actually two groups closely approximated, slightly notched behind) separated from vomerine series by a narrow space; palate with a minute medial perforation (opening of gland situated on top of head); limbs large, when adpressed, separated by 3.5 costal folds (limbs in males and younger specimens may be separated by only 2.8 to 3 costal folds); hands and feet broad, the three or four outer toes about half webbed, their broad truncate tips free; inner finger and toe not free; a postiliac gland, whitish in life; tail slightly shorter than head and body (certain other large specimens have the tail slightly longer than body); thirteen costal grooves present, the first somewhat obscured.

Color: Head and body nearly uniformly black with a few flecks of light red-brown on limbs, and some gray or cream flecks on sides of tail and under tail. Ventral surfaces black or slate black; base of tail surrounded by a cream ring.

Measurements in mm.: (see table).

Remarks: Specimens were found chiefly in rotting logs and stumps; however, two were taken under trash, and one under a fallen palm. They were sluggish in their movements and sometimes permitted themselves to be picked up without showing fear or making an effort to escape.

An examination of the stomach of the specimen here described disclosed numerous ants and beetles recently ingested.

TABLE OF MEASUREMENTS AND DATA FROM MAGNADIGITA ROBUSTA

COLLECTION	KUMNH	KUMNH	RCT	RCT	RCT	RCT	RCT	RCT	RCT	RCT
Locality	Isla Bonita	Isla Bonita	Isla Bonita	Isla Bonita	Cervantes	Isla Bonita	Cervantes	Cervantes	Isla Bonita	Isla Bonita
Number	25074	25071	663	662	1027	1434	1026	289	1433	1432
Sex	♀	♀	♀	♀	♀	♂	♂	♀	yg.	yg.
Snout-vent length	110	107	105	105	95	78	66	59.5	40	37
Snout to foreleg	29	28.6	28.2	27.2	25.2	22	19.4	17.2	13	12
Axilla to groin	63	59	58	61	54	46	34.4	32.8	21	20.5
Tail	112.5	103	111	96	106	91	65	48.5	31	25
Arm	22	22	22	20	20.5	17	15	12.2	8	8.5
Leg	23	23	23	21.5	21.6	20	17	13	8.3	8
Head width	19.5	18	16.8	18	15.2	13.5	12	10.5	6.8	7
Head length (gular fold)	23	23	22.7	21.6	19.4	17.3	16	13	9.5	8
Head width in body length	.....	6	5.6	5.8	6.25	5.77	5.5	5.66	5.88	5.3
Head length in body length	.....	4.65	4.62	4.8	4.9	4.5	4.1	4.6	4.2	4.6
Arm in body length	.....	4.86	4.77	5.2	4.63	4.6	4.4	4.88	5	4.4
Leg in body length	.....	4.65	4.57	4.4	4.4	3.9	3.88	4.57	4.8	4.1
Costal grooves	13	13	13	13	13	13	13	13	13	13
Maxillary teeth	53–52	51–53	49–49	46–46	43–42	34–36	30–31	30–28	15–14	14–14
Premaxillary teeth	10	7	10	11	.....	4	4	5	1	3
Prevomerine teeth	20–18	20–21	19–17	18–19	15–16	14–14	17–15	20–13	9–10	7–6
Paravomerine teeth	199–199	200–212	157–157	188–188	134–132	112–112	74–74	88–88	50–50	57–57
Mandibular teeth	66–66	64–64	63–63	56–56	54–54	42–42	38–38	.....	23–23	17–17

Specimens are available from the following localities: Cervantes, 5000 ft., K.U.M.N.H. 1, R.C.T. 3; Isla Bonita, 5600 ft., K.U.M.N.H. 7, R.C.T. 5.

The known distribution of this species includes the following localities: La Palma (in depression between Volcán Irazú and Volcán Barba, *circa* 6000 ft.); Carillo, northeast of Volcán Barba (elevation ?); Rancho Redondo, northwestern slope of Volcán Irazú (5000 ft.); Navarro, south of Cartago ("collections were made in forests up to 6000 ft."). The elevation of Carillo is approximately 1500 ft., but I surmise that the specimen came from a considerably higher elevation nearby.

The species seems to be largely confined to the central group of volcanoes, specimens being usually found at an elevation of between five and six thousand feet.

Collecting in the Talamanca Mountain chain disclosed no specimens; and it may be doubted that the species occurs in that range. However, specimens reported from Navarro suggest that the species may occur, since this locality is south of the drainage of the Reventazón and there is little break in the elevation between the mountains near Navarro and the southern mountain range.

Genus Bolitoglossa Duméril, Bibron and Duméril

Bolitoglossa (*part.*) Duméril, Bibron and Duméril, Erpétologie Générale, vol. 9, 1854, p. 88.

Type of genus: *Bolitoglossa mexicana* Duméril, Bibron and Duméril [= *Salamandra platydactyla* Gray].

The number of species of this genus occurring in Costa Rica is probably six.

Key to Costa Rican Species of Bolitoglossa

1. A ridge or fold crossing frontal region and eyelids; the maxillary teeth greatly reduced or absent ..... *colonnea*
   No ridge or fold across frontal region; maxillary teeth usually numerous 2
2. Vomerine teeth in two elevated ridges, the teeth arranged in more than a single series tending to form a patch ..... *palustris*
   Vomerine teeth on two elevated ridges in a single series not tending to form a patch 3
3. Dorsal surface light cream, with darker pigment forming indefinite stripes on the dorsum, and to a lesser extent on venter *striatula*
   Dorsal surface lacking stripes; a dark lateral stripe may be present, 4
4. Sides of body, tail and ventral surfaces blackish; dorsal surface yellowish or orange, on which there may be two or three ir-

regular blackish lines or lines broken into small separate spots; costal grooves strongly defined ..... *platydactyla*

Ventral surfaces not black; no black dorsal stripes or linear series of black dots; grooves variable 5

5. Venter cream without markings; dorsum with irregular cream lines dark edged or dark-edged cream spots on a lavender ground color; costal grooves distinct ..... *flaviventris*

A grayish black lateral band; venter pigmented with fine whitish flecks or very short longitudinal lines; costal grooves rather indistinct ..... *lignicolor*

[*Bolitoglossa platydactyla* (Gray)]

Salamandra platydactyla Gray, Supplement, *in* Griffith and Pidgeon, Cuvier's Animal Kingdom, vol. 9, 1831, p. 107.

Bolitoglossa platydactyla Taylor, Univ. Kansas Sci. Bull., vol. 30, 1944, p. 219.

Spelerpes variegatus Günther, Biologia Centrali-American; Reptilia and Batrachia, Jan. 1902, p. 302 (*part.*), (reports a specimen in Natural History Museum, labeled *Spelerpes morio*, as belonging to this species. Underwood coll.); ? Cope, Proc. Amer. Philos. Soc. vol. 31, 1893, p. 335 (Buenos Ayres, Costa Rica).

Oedipus platydactylus Dunn, The Salamanders of the Family Plethodontidae, Smith Col. Publ., 1926, pp. 400-405, 440-441 (*part.*). (A specimen mentioned in the British Museum from San Carlos is stated to be "*certainly platydactylus*"; two specimens in the British Museum are reported from Medellin, Colombia.)

The confusion of species under the names *platydactyla* and *variegata* is considerable. I have seen no specimen of this species or closely related forms from Costa Rica. Dr. Emmet Reid Dunn, who examined the Günther specimen from San Carlos states that it "is certainly *O. platydactylus* rather than any other described form. It has a rather broken dorsal light band."

Until specimens of the San Carlos form are rediscovered in Costa Rica, the place of this name, for a species in the fauna of Costa Rica, must be uncertain. Dunn has placed certain species, recognized by subsequent authors, in the synonymy of *platydactyla*.

Bolitoglossa flaviventris (Schmidt)

Oedipus flaviventris Schmidt, Zool. Ser. Field Mus. Nat. Hist., vol. 20, 1936, pp. 148-150 (type locality, Chicharras, Chiapas, Mexico).

Bolitoglossa flaviventris Taylor, Univ. Kansas Sci. Bull., vol. 30, 1944, p. 219 (Tonolá).

Spelerpes salvinii Brocchi (*nec* Gray), Mission Scientifique au Mexique et dans l'Amérique Centrale; Étude des Batraciens de l'Amérique Centrale, livr. 3, 1883, p. 117, pl. 18, figs. 3, 4.

Oedipus salvinii Dunn, The Salamanders of the Family Plethodontidae. Smith Col. Publ., 1926, pp. 405-408, map 74 (*part.*); Taylor, Univ. Kansas Sci. Bull., vol. 25, 1938 (1939), pl. 28, figs. 2, pp. 296-297.

The species is included in the Costa Rica fauna on the basis of specimens from Miravalles and Banana, C. R.

Diagnosis: A medium-large form, the snout-vent length reaching 86 mm.; the tail 90 mm.; digits completely webbed, the front outline of hand and foot appearing scalloped; vomerine teeth in two curving series of usually 15-17 teeth each, almost meeting mesially; head wider than body, flattened, truncate, its width in snout-vent length 6.75 to 7.75 times. Lavender-brown with a brown bordered cream dorsolateral stripe, and a similar median stripe; stripes may be broken into spots.

Description of species:—(U.S.N.M. No. 37772, Marivalles, Costa Rica). Head truncate oval, a little wider than body its width in snout-vent length approximately 7.6 times; length of eye slightly greater than its distance from nostril; posterior part of eyelids inserted under a diagonal fold; a subnarial swelling on lip; the angle of the jaw extends considerably behind back level of eye; a strong gular fold present, the nuchal groove arising from it can be traced up a short distance on side of neck; a groove from side of head crosses jaw angle and chin; a weak postorbital groove reaches down and back to the beginning of nuchal groove; 13 costal grooves, counting one in axilla and groin; a very large submental hedonic gland; no sublingual fold (the floor of the mouth has been injured and that which appears to be a fold is not so); vomerine teeth 9-10, beginning beyond outer level of choanae, curve in diagonally and are separated mesially by a space equal to less than diameter of a choana; maxillary teeth present, the number approximately 18-18 counting spaces where teeth are missing; 2 premaxillary teeth pierce the gum (perhaps a third has been present); paravomerine teeth in a single patch, notched behind; mandibular teeth 18-18.

Limbs strong, the hands and feet flattened, fully webbed with the tips of digits giving their outer edges a scalloped appearance; when adpressed, the limbs separated by a little less than four costal folds.

Color: Generally lavender-brown; on each side of back a sinous white (cream) stripe bordered above and below by brown; a similar median stripe; tail white above with rounded brown spots, the white, bordered laterally with brown; venter, chin and throat white (cream).

Measurements in mm.: Snout to end of vent 61.5; width of head 8.1; length of head 12; tail 56.8; arm 15.2; leg 17.

Remarks: The described specimen is faded and somewhat softened and certain details are obscured. I have referred the specimen

to *flaviventris* largely on the basis of the immaculate ventral surfaces. That the reduced number of vomerine teeth in this specimen is significant, is doubtful.

I have seen a female specimen from Banana, Costa Rica, that has slightly longer legs separated by only 1 to 2 costal folds; there are 8 premaxillary teeth, none piercing the lip, but standing near the edge of the lip. The dorsolateral stripes are broken up into spots. The small number of specimens from these southern localities throws little or no light on the relationship of *Bolitoglossa flaviventris* and *Bolitoglossa salvinii*. The species is frequently found on banana plants or in bromelias.

Bolitoglossa lignicolor (Peters)

Spelerpes (Oedipus) lignicolor Peters, Monatsb. König. Akad. Wiss. Berlin 1873, p. 617 (type locality, Chiriquí, Panamá, H. Ribbe coll.); Sitzungsb. König. preus. Akad. Wiss. Berlin, 1882, p. 117.

Oedipus lignicolor Dunn, Zool. Ser. Field Mus. Nat. Hist., vol. 12, 1924, pp. 99, 100; Salamanders of the Family Plethodontidae, Smith Coll. Publ., 1926, pp. 410-413 (*part.*); Copeia, 1937, No. 3, p. 163 (Boquete [Panamá]); Proc. Acad. Nat. Sci. Philadelphia, vol. 92, 1940, p. 105 (Puerto Armuelles, Panamá; states that he thinks *Oedipus ahli* Unterstein "a straight synonym").

Spelerpes lignicolor Günther, Biologia Centrali-Americana; Reptilia and Batrachia, Jan. 1902, pp. 302-303 (Chiriquí, Panamá).

Diagnosis: A form related to *Bolitoglossa yucatana* and *Bolitoglossa palustris* but having the vomerine teeth in two series, not reaching outer end of choanae, and the teeth in each, in a single row. The tail is slightly shorter, equal, or slightly longer than head and body; a grayish-black lateral band reaching high on sides is continuous with the dark ventral coloration. Venter with fine whitish flecks or short longitudinal lines.

Description of species: Head width contained in snout-to-vent length approximately 5½ times; eye shorter than its distance from tip of snout; a pair of subnarial swellings, larger in male than female; vomerine teeth 11-14 in two series, the teeth in each in a single row, beginning near middle of choanae, curving in and back, and separated from its fellow by width of a choana; paravomerine teeth in a single patch, notched behind; 13 costal grooves, usually not very distinct.

Maxillary teeth from as few as 6-6 (U.S.N.M. No. 58491 Boquete, Panamá) to 24 in another Panamá specimen from Chiriquí; no sublingual fold; the groove from eye to the nuchal fold obsolete, sometimes present for a short distance behind eye; a gular fold, but there is no white line concealed by it; a glandular spot (lavender) behind insertion of hind limb; arms and legs separated by 2½ to 3

costal folds, when adpressed; the epibranchial cartilage forms a fold, distinct the length of two costal folds behind posterior level of arm insertion; eye nearly a third longer than the axial snout length; tail constricted at base.

Color: (from types). Above, from snout to tip of tail, yellow brown, speckled with darker pigment, which here and there forms lines; in one of the two cotypes there is a mid-dorsal line on neck that divides anteriorly. Below and on sides, color grayish black sharply set apart from color of dorsum, and sprinkled more or less with small white or yellow flecks which on under side of neck and chin region unite to form fine longitudinal lines.

Measurements in mm.: (type specimen). Total length 100; tail 48; head to end of vent 52; head width 9.5; head length 9.5; snout to arm insertion 17; axilla to groin 29; arm 12; hand 4; leg 13.5; foot 5.

Remarks: A specimen from Chiriquí, Panamá, is described as follows by Günther (*loc. cit.*): Tail cylindrical longer than head and body; the series of palatine [vomerine] teeth nearly meet in the middle and do not extend outwards beyond choanae; black of back forming indistinct longitudinal bands, throat and chest with minute whitish specks. The type description omits many important characters. Peters states that the teeth [vomerine teeth and paravomerine teeth] are similar to a published figure of *Spelerpes Belli* save that there is but a single series of paravomerine teeth. Since in the figure the vomerine teeth are in a single continuous line, one presumes that this condition obtains in the type of *lignicolor.* The two chief characters, which seem to separate *Bolitoglossa palustris* from this species is that each of the ridges has the vomerine teeth arranged in a patch or multiple series, rather than in a single line, and the tail is much shorter than head-body length (approximately .7).

Dunn reports a Costa Rican specimen from Sarapiquí in his discussion of *lignicolor* (*loc. cit.*) that has the vomerine teeth in a patch. I suspect that the badly mutilated specimen, A.M.N.H. No. 11725, may be a specimen of *palustris.* The bones however are green in color, and this is not true of the bones of *palustris.* It may be significant that *yucatana* has the vomerine teeth similarly arranged.

Bolitoglossa palustris Taylor

Plate LXXXII

Bolitoglossa palustris Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 1, Apr. 20, 1949, pp. 283-284 (type locality, San Isidro El General, Costa Rica, E. H. Taylor, coll.).

Diagnosis: A member of the rufescens group, with a short broad head; fully webbed or palmate hand and foot; vomerine teeth total 34 on two strongly-elevated ridges, in more than a single series, beginning about level of middle of choanae; choanae large; maxillary teeth 14-14; premaxillary teeth 4; no free sublingual fold under tongue; costal grooves indistinct, probably 13; tail shorter than head and body.

Description of type: Snout moderately short, truncate, moderately elevated above the mouth; subnarial swellings small, distinct; nostril small; canthus rostralis rounded, the loreal region sloping abruptly to lip; diameter of eye greater than length of snout, about equal to its distance from middle of tip; surface of snout on a level with interorbital and occipital surfaces; interorbital width, equal to twice width of eyelid; upper eyelid not overlapping lower, behind eye, the ends not fitting in a small groove; a postorbital groove or depression reaching back to a vertical groove from side of chin which crosses the angle of jaw but fails to reach the top of head, nor is it continuous across chin; a very well-defined gular fold, but nuchal grooves from ends of fold not or scarcely traceable on sides of neck, and definitely not reaching to median nuchal line; angle of mouth reaching slightly behind posterior level of orbit; posterior extension of epibranchial cartilage forming an elevated fold which reaches back of arm insertion, half the length of arm.

Maxillary teeth 14-14 (possibly two or three more as evidenced by breaks in the continuity of the series); 4 premaxillary teeth; vomerine teeth 16-18, in two series (each arranged in more than a single irregular row) beginning at the level of middle of choanae, and curving slightly, separated mesially by a distance equal to greatest diameter of choana; their diameter contained in distance between them, three and one-half times; paravomerine teeth in a single subtriangular patch, the length only about a third greater than width, not notched behind, separated from the vomerine series by a distance greater than half distance between choanae; teeth strong forming typical chevron-shaped series; some pigment in evidence in anterior palatal region, at side of paravomerine teeth and on floor of mouth anterior to tongue.

Dorsal surface of back rather rough; side and venter smooth; costal grooves rather indistinct, seemingly 13 present; adpressed limbs separated by 3½ folds; a constriction at base of tail; 25 caudal grooves present; tail tetragonal in cross section, compressed pos-

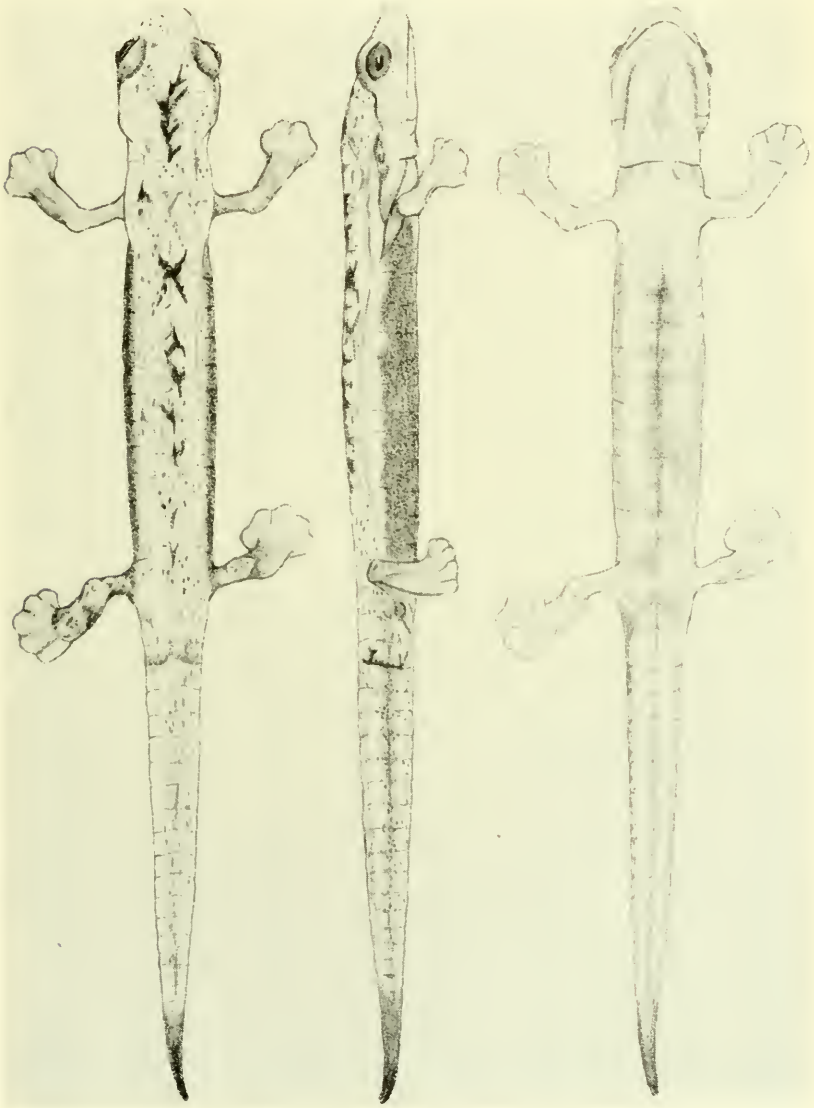

PLATE LXXXII. *Bolitoglossa palustris* Taylor. Type, K.U.M.N.H. No. 23817, San Isidro El General, Costa Rica. Total length, 81.8 mm.

teriorly, with a subcaudal groove present; anal folds present on sides of cloaca; small glandular area behind insertion of hind limb, dark in color.

Color: In life, above entire dorsal surface of head and tail buff to fawn with minute irregularly scattered flecks of brown, and some few very small irregular spots, that on back of occiput most distinct; dusky low on sides of neck and body (under a lens the black pigment is nearly uniformly distributed save for some minute dashlike areas where pigment is wanting); venter dusky, but lighter than sides, with numerous very narrow, more or less elongate lighter spots; sides of tail lighter than body but with some brownish flecks.

Measurements in mm.: Total length, 81.8; snout to vent, 48.8; tail, 33; snout to arm insertion, 14; snout to gular fold (median), 12; width of head, 8.3; axilla to groin, 25.3; arm, 11.1; leg, 11; width of head in snout-vent length, 5.88 times.

Remarks: In the original description, the loss of a page from the submitted manuscript is responsible for the absence of the color characters and measurements of the type. See comments under *Bolitoglossa lignicolor.*

Bolitoglossa striatula (*Noble*)

Plate LXXXIII

Oedipus striatulus Noble, Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 344-346, pl. 19 (type locality, Cukra, eastern Nicaragua, Halter and Mannhardt collectors, AMNH No. 6999 [specimens also reported from Chontales Mountains, Mt. Mombacho, Nicaragua, and Turrialba, Costa Rica]); *idem*, vol. 44, p. 2; Dunn, Field Mus. Nat. Hist., Zool. Ser., vol. 12, no. 7, May, 1924, pp. 99, 100 (key); The Plethodontidae, 1926, pp. 416-418, map, fig. 78 (type series; also two specimens listed from Surubres, Costa Rica).

Bolitoglossa striatula Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, May 15, 1944; pp. 195, 219-222; *idem*, vol. 33, pt. 1, April 20, 1949, pp. 279, 280, 281.

Diagnosis: Medium-sized salamanders (62 mm.); costal folds 13, not strongly marked; vomerine tooth rows arranged in a single line; vomerine teeth total 22-24; maxillary teeth in large adults total 38 to 46. Color on dorsum buff or fawn, with dark pigment arranged in longitudinal lines or stripes; lighter beneath but some lineation evident.

Description of species: (From R.C.T. No. 127.) Head large, broader than body; snout gently rounding and extending beyond mouth for 1.2 mm.; eye length (edge of upper eyelid) slightly longer than snout, but not quite equal to distance from eye to the median tip of snout; dorsal surface of head nearly flat; interorbital

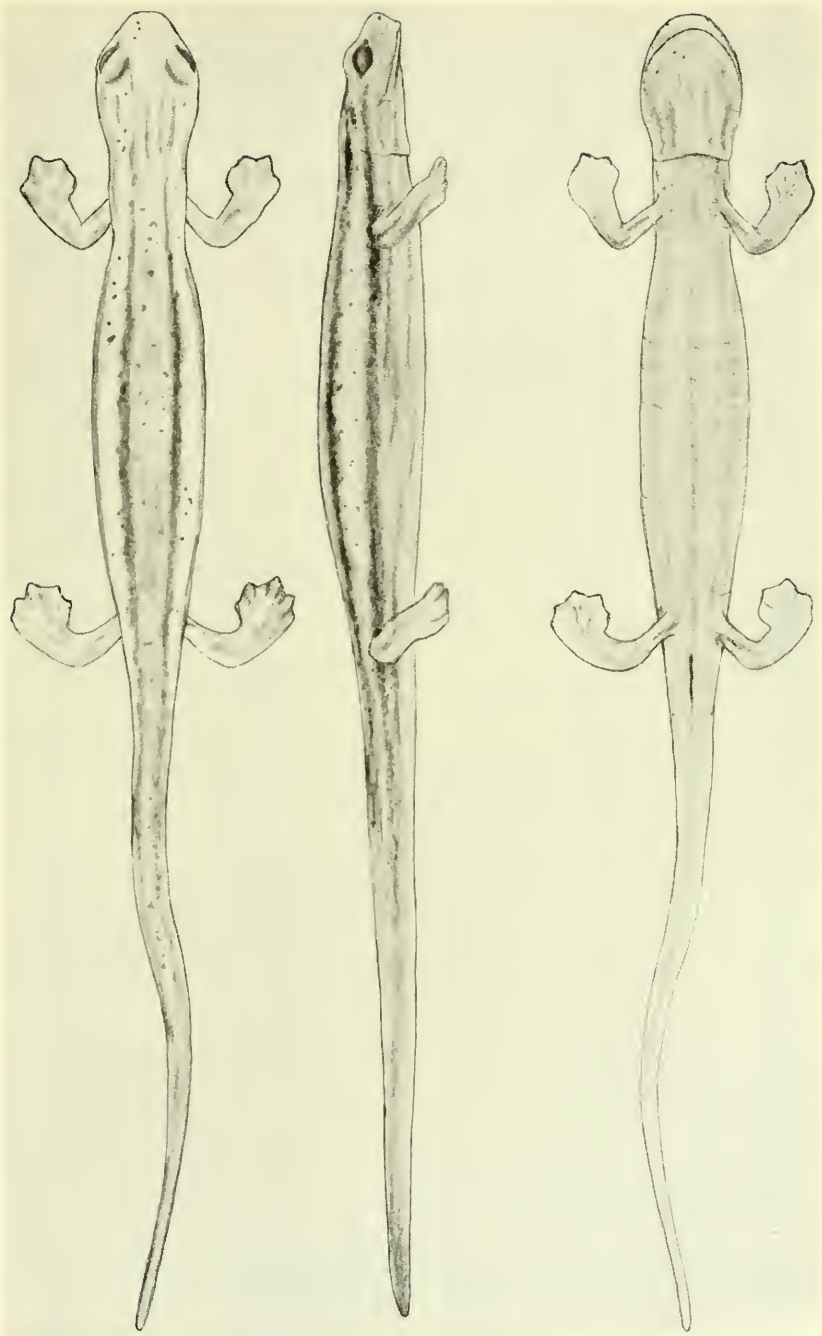

PLATE LXXXIII. *Bolitoglossa striatula* (Noble). R.C.T. No. 127. Turrialba, Costa Rica. Total length, 123.5 mm.

TABLE OF MEASUREMENTS AND DATA ON BOLITOGLOSSA STRIATULA

COLLECTION	RCT	RCT	KUMNH	RCT	KUMNH	RCT	RCT	RCT	KUMNH	KUMNH
Number	127	1425	25076	1431	25077	1427	46	128	25079	25081
Sex	♀	♀	♀	♂	♀	♀	♂	♂	♀	♀
Snout to vent	62	62	58.6	53.5	53.2	51	50.2	50	41	34
Snout to foreleg	17	17	17	16	16	14.8	14.6	15	14	10.2
Axilla to groin	37	37	33	29	30	29	28	27.5	21	16
Tail	61.5	66	60	61.5	57	50.5	52	50	40	28
Arm	12.2	12.6	12.4	12	11	11	11	10.5	8.8	7
Leg	12.8	13.6	12.8	12	12	11	11	11	8.8	7
Head width	9.5	8.9	8.7	8.8	8.2	8	8	8.1	7	5.5
Head to gular fold	13.6	13	13	12.2	11.5	11	11	11.3	10.2	8.3
Head width in length	6.5	6.9	6.9	6	6.48	6.3	6.2	6.1	6	6.2
Head length in length	4.58	4.8	4.5	4.4	4.6	4.6	4.4	4.4	3.7	4.1
Costal grooves	13+	13	13	13	13	13	13	13	13	13
Maxillary teeth	19–19	15–19	23–21	22–23	15–16	19–21	18–18	16–13	12–13	7–7
Premaxillary teeth	3+	2+	1+	5	1	2+	5	5	3	2
Prevomerine teeth	11–12	12–12	11–12	12–11	12–10	8–11	7–9	9–7	10–8	9–9
Paravomerine teeth	99–99	101–97	87–87	95–97	77–81	72–65	64–75	84–86	62–68	47–53
Mandibular teeth	37–36	41–38	37–38	40–41	33–35	35 (?)	31–33	37–36	30–32	23–24

width 1.7 times transverse width of upper eyelid; posterior ends of eyelids tucked under a diagonal fold; postorbital groove not discernible (evident in certain specimens but never clearly defined); groove crossing end of jaws cannot be traced on chin save as a very slight depression; gular fold across throat curving forward very slightly; lateral nuchal grooves arising from ends of gular fold absent or not clearly defined.

Maxillary teeth rather small, 19-19; premaxillary teeth 5; vomerine teeth 11-12 in two elevated, arched series, curving back mesially and separated by space equal to that between two teeth; mandibular teeth 37-36; paravomerine teeth 198 in a single compact patch (convex rather than flat), the teeth arranged more or less in chevrons (new teeth being added laterally and anteriorly); palatal area anterior to the prevomers vaulted with a minute median opening; choanae large, the diameter of one choana in distance between choanae about 3.7 times; tongue free, papillate; lacking a sublingual fold.

Costal folds and grooves dim or obsolete (13 grooves present and 12 folds normally present); behind arm, grooves obscured by the posterior extension of the epibranchial that reaches above the arm forming a distinct elevated fold; tail (61.5 mm.) very slender and somewhat compressed, about equal to distance from snout to vent (61 mm.); 26 + costal folds, the terminal portion of tail being undifferentiated; width of head (9.5 mm.) in snout-vent length, 6.5 times; head length to gular fold (13.6 mm.), in snout-vent length, 4.58 times.

Hand and foot palmate, the digit tips slightly triangular, with slight emarginations between toes; arm and leg when adpressed separated by 2.5 to 3 costal folds; postiliac gland absent or indiscernible.

Color: Body yellowish to cream; a broad median brownish cream stripe bordered laterally by a dark streak; dorsolateral cream stripe bordered below by a broad brownish stripe edged with black where it borders the cream; venter with two narrow outer dim longitudinal streaks and a median dim darker streak; some black dots or streaks on back of head, on the middorsal stripe and on tail; some trace of the body marking may extend onto the tail.

Measurements in mm.: (See table).

Variation: Males probably do not attain the maximum size of females. On the chin the hedonic gland is in evidence but it is not strongly differentiated since the glandules of the skin in that region are somewhat larger and thicker than elsewhere. The areas

about the nostrils are much swollen, the tip of the snout being swollen and sharply truncate. The maxillary teeth are a little larger than those in females and the premaxillary teeth are very much larger and farther forward, piercing the lip, and visible when the mouth is closed.

All specimens were taken at the farm of the Inter-American Institute of Agriculture. There are five specimens in the R.C.T. Collection.

Remarks: Specimens were taken in daytime from under piles of grass and weeds. At night they were found crawling about on shrubs or vines not far from the margin of a pond, or on the vegetation above rainpools. They were active especially on rainy nights.

Thirteen specimens are at hand, all captured on the I.A.I.A. Farm at Turrialba. I believe that this town and Surubres are the only known localities for the species in Costa Rica. This is perhaps surprising since the species is known from several localities in Nicaragua.

Bolitoglossa colonnea (Dunn)

Plate LXXXIV

Oedipus colonneus Dunn, Field Mus. Nat. Hist., Zool. Ser., vol. 12, no. 7, May 19, 1924, pp. 96-97 (type locality, La Loma, on trail from Chiriquicito to Boquete, 2000 ft., Bocas del Toro, Panamá); The Plethodontidae, Smith College Publ., Northampton, Mass., 1926, pp. 420-422 (type only listed with one other questionably identified specimen).

Bolitoglossa colonnea Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, May 15, 1944, p. 219 (referred to *Bolitoglossa*).

Diagnosis: A small species with a small ridge or fold across forehead and eyelids. Maxillary teeth greatly reduced or absent; costal grooves very indistinct or absent; adpressed limbs separated by a distance of 10 mm.

Description of species: (K.U.M.N.H. No. 29966 ♀). Head as wide as body, with a slight nuchal constriction; snout truncate seen from above, the edge extending .7 mm. beyond mouth; nostrils small with strongly-swollen areas below nostrils forming slight projections; snout surface corrugated or roughened, with small elevated patches, to a point just back of front level of eyes, where the surface becomes suddenly elevated .2 to .3 mm.; edge of elevation somewhat roughened, uneven, suggesting a fleshy fold, extending onto eyelid; upper eyelid thickened, fleshy, its width in interorbital width 1.6 times. Cloacal walls with strong folds.

A groove or depression from back of eye curves down across posterior angle of jaw and may be traced across the throat; an ample

PLATE LXXXIV. *Bolitoglossa colonnea* (Dunn), K.U.M.N.H. No. 29966, Los Diamantes, 1 mi. S Guápiles, Costa Rica. Total length, 86.5 mm.

gular fold (width .5 mm.), the lateral nuchal grooves more or less indicated to middorsal line; posterior extension of epibranchial cartilage reaches above and behind arm insertion a distance of 3 mm.; a fine indistinct fleshy fold or groove passes from eye back along side of neck.

Maxillary teeth absent on one side, two on the other side; premaxillary teeth five; prevomerine teeth 13-13, on two elevated, somewhat arched rows curving back mesially, somewhat irregularly arranged rather than being in a continuous row, separated from the paravomerine teeth; latter in a single regular patch, the teeth numbering approximately 178; mandibular teeth small 30-30; the palatal area in front of the vomerine teeth is not strongly arched, a depression but no distinct perforation evident; choanae moderately large, the diameter of one in interchoanal distance four times; tongue small, free, no trace of a sublingual fold.

Hands and feet completely palmate, slightly emarginate between digits; third finger and toe pointed; limbs when adpressed separated by approximately 10 mm. Costal grooves not evident, the number of vertebrae (which may be counted) suggest the equivalent of 13 grooves and 12 folds; tail thin, compressed toward tip; its length .81 percent snout-vent length; the width of head in snout-vent length 6 times.

Color: Brownish gray above and on sides, streaked with darker; lighter below on venter, the color nearly uniform; markings on head outline a pentagonal area and forming an X-shaped mark; two very indistinct lateral streaks with some mottling on back; arms and legs darker, blackish brown, the hands and feet cream, lightly pigmented.

Measurements in mm.: See attached table.

Variation: A young male, R.C.T. No. 1407, has a sharply truncate snout with large mammalike swellings below the nostril directed somewhat forward, forming the two most anterior points of the snout seen from above; seen from in front or from below one notes

MEASUREMENTS AND DATA ON BOLITOGLOSSA COLONNEA

COLLECTION	KUMNH	RCT	KUMNH	RCT
Number	29966	1409	29967	1407
Sex	♀	♀	♀	♂
Snout-vent length	47.5	40	39.7	29
Snout to foreleg	13.2	11	11	8.9
Axilla to groin	27	23	22	14
Tail	39	38	32	27.2
Arm	9	8	9	7
Leg	9.8	8	9	7.4
Head width	7.9	6.2	6.3	5.6
Head length (to gular fold)	10.4	9	9	7.5
Head width in body length	6	6.48	6.3	5.2
Head length in body length	4.57	4.4	4.4	3.9
Arm in body length	5.3	5	4.4	4.1
Leg in body length	4.84	5	4.4	3.9
Maxillary teeth	2-0	6-?	0	0
Premaxillary teeth	5	6	2	2
Prevomerine teeth	13-13	13-11	12-12	8-9
Paravomerine teeth	178	168	168	114
Mandibular teeth	30-30	29-29	.....	19-20

a deep depression between the swollen elevations, at the lower level of which two teeth emerge through the lip. The dorsal coloring is lighter, brownish cream, but the markings of the adult are in evidence; cloaca strongly papillate. Another female specimen, R.C.T. No. 1409 (approximately the size of the type), has markings as described here; the upper of the two lateral streaks beginning on neck is deep black at its beginning. The dermal fold or ridge across the head and eyelids is in evidence in all the specimens, the area of the snout in front of the fold being on a lower level than the interorbital and occipital region. The area behind the fold is pentagonal in shape, drawn out to a sharp angle behind, and outlined in darker color in all of the specimens. Six maxillary teeth are present on one maxilla, but I cannot determine whether or not teeth have been present on the opposite side. In K.U.M.N.H. No. 29967, no maxillary teeth can be found. Teeth are said to be absent in the type.

Remarks: This lowland form, originally described from the Caribbean side of Panamá (La Loma, Bocas del Toro), was discovered at Los Diamantes, 1 mile south of Guápiles on the eastern side of Costa Rica. These specimens, four in number, were taken at night either crawling on fallen logs or on plants near a small fast-flowing stream. They were sluggish, and made little struggle to escape when picked up.

Genus PARVIMOLGE Taylor

Parvimolge Taylor, Univ. Kansas Sci. Bull., vol. 30, 1944, pp. 223, 226.

Type of genus: *Oedipus townsendi* Dunn.

There must be some doubt as to the correct generic placement of the following Costa Rican form until its skeletal characters are known. As yet only a single specimen has been taken.

Parvimolge richardi Taylor

Plate LXXXV; text fig. 4

Parvimolge richardi Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 1, Apr. 20, 1949, pp. 284-285 (type locality, Isla Bonita [American Cinchona Plantation] Volcán Poás, elevation approximately 6500 ft., R. C. Taylor, coll.).

Diagnosis: A member of the genus *Parvimolge*, but differing from *Parvimolge townsendi* in the absence of the series of enlarged dorsal glands, but agreeing in the ossification of the skull and the modification of the digits, diminutive body size, moderately enlarged nostril, presence of maxillary teeth, and absence of an orbitolabial groove.

Snout rather pointed; digits grown together, tips of fingers and toes pointed; tail not constricted at base; chin with an arched groove; nostrils enlarged; thirteen costal grooves; five to six costal folds between adpressed limbs; paravomerine teeth in a single patch,

PLATE LXXXV. *Parvimolge richardi* Taylor. Type, R.C.T. 1436; Isla Bonita, Costa Rica. Total length, 49.5 mm.

not notched behind; vomerine teeth on strongly elevated ridges; twelve maxillary teeth on each side; six premaxillary teeth.

Description of type: (R.C.T. No. 1436). Female; snout bluntly pointed; eye very large, its horizontal diameter a little more than one and two-fifths times length of snout; nostril circular, moderately enlarged; interorbital width about equal to an eyelid; surface of head smooth, the openings of skin glands scarcely evident save in a curved series on forehead, between and partly anterior to eyelids.

Gular fold with an irregular nuchal groove passing up on each side of head and meeting its fellow on the median line; on chin two

FIG. 4. *Parvimolge richardi.* Type. Upper. Left hand, dorsal and ventral views. Lower. Left foot, dorsal and ventral views.

grooves arching forward (seemingly without a groove across base); on each side of the base, a groove passes up across the angle of the jaw to the dorsal surface of the head, then turns diagonally backward and joins its fellow on middorsal line somewhat in front of nuchal groove; a dim groove runs from eye back to nuchal groove on side of head; thirteen costal grooves; fold caused by posterior extension of the epibranchial cartilage reaching as far as third costal fold; paravomerine teeth form a single elongate patch, widened and rounded posteriorly, coming nearly to a point anteriorly, separated

from vomerine series by a short hiatus; vomerine teeth on two elevated ridges about eight on a side, narrowly separated mesially; maxillary teeth about 12-12 not reaching back as far as middle of eye; six premaxillary teeth; about 16-16 mandibular teeth.

Adpressed limbs separated by six costal folds. Limbs small, weak, the hands and feet small; digits grown together rather than webbed. Third finger proportionately very large, the pointed tip extending more than a third of its length beyond other finger; tip of second finger free, while those of the first and fourth are not or scarcely free. Foot with the first and fifth toes not free; terminal joint of the second and fourth toes free, third toe proportionally large, the tip extending beyond other toes for nearly one third of its length.

Sides of the cloaca with smooth diagonal folds (female).

Color: Above brownish lavender, darker on the head, especially on upper eyelids, dorsally growing lighter to the base of the tail; a very indefinite darker lateral line; lower part of sides as light or lighter than dorsum; under side of chin and abdomen light lavender with very numerous white or cream flecks; anal region light; tail dark with numerous lighter flecks or vermiculations. The small postiliac spot behind insertion of leg scarcely discernible; white flecks below nostril and eye; a white line on tip of snout.

Measurements in mm.: Total length, 49.5; snout to vent, 28; snout to foreleg, 7.6; tail, 22; head width, 4.9; length of head to gular fold (ventral), 5; length to gular fold (lateral), 5.85.

Remarks: This specimen was taken at Isla Bonita near the base of a stump under bark by Richard C. Taylor. It was found in company with *Chiropterotriton abscondens.*

The absence of the enlarged glands on the back show that, while generically related, *Parvimolge townsendi* and *richardi* are widely distinct specifically. The bluntly pointed snout likewise is a differentiating character easily discerned.

Genus HAPTOGLOSSA Cope

Haptoglossa Cope, Proc. Amer. Philos. Soc., Dec. 23, 1893, p. 33.

Type of genus: *Haptoglossa pressicauda* Cope.

Cope originally placed the genus in the subfamily Thoriinae, "hence the vertebrae are opisthocoelous and the carpus and tarsus not ossified. Tongue adherent in front and by the middle. Digits not distinct, 4, 5."

The type is lost and its place in the plethodontid salamanders must await its rediscovery.

Haptoglossa pressicauda Cope

Haptoglossa pressicauda Cope, Proc. Amer. Philos. Soc., vol. 31, Dec. 23, 1893, pp. 333-335 (type locality, Palma, Costa Rica, "near the Golfo Dulce" on the Pacific slope); Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, May 15, 1944, pp. 229-230.

Oedipus uniformis Dunn, The Salamanders of the Family Plethodontidae. Smith College Publ., 1926, pp. 427-430 (*part.*).

Diagnosis: A diminutive salamander, 31.5 mm. snout to vent; tail about as long as body (without head); digits not distinct; tongue adherent in front and by the middle; limbs very small; nineteen indistinct costal folds.

Description of species: "Form slender, limbs very small. Length of tail equals that of the body without the head. Length of head contained in that of the body to the vent, seven and a half times; the width less than the length. A gular and nineteen costal folds, the latter not very distinct. Fore and hind limbs each equal to three intercostal spaces. Digits indicated by emarginations of the foot border. Vomerine teeth in two moderately arched transverse series, not produced posteriorly on the middle line, hence well separated from the rather wide single patch of parasphenoid teeth. Tongue rather small, oval. Nostril of moderate size, situated well anteriorly. Eye, large. Tail compressed from near base to apex, with a median dorsal, but no ventral groove, and well-marked vertical grooves."

Color: "Uniform black; underside of head and tail a little paler than other regions."

Measurements in mm.: Total length 62; length to posterior angle of mouth 4; length to fore limb 8; length to hind limb 28.5; length to base of tail 31.5; width of head at angle of mouth 3.

Remarks: Cope states that the species superficially resembles species of *Thorius* and *Oedipina*. Dunn has placed the species as a questioned synonym of *Oedipus uniformis* without adequate reason. The type is presumably lost (Dunn states, "the type has been destroyed"). The species has not been rediscovered.

Genus OEDIPINA Keferstein

Oedipina Keferstein, Nachricht. Ges. Wiss. Göttingen, 1868 Aug. (*fide* Günther), p. 331.

Type of genus: *Oedipina uniformis* Keferstein.

The genus as here treated has the following species known from territory outside of Costa Rica:

1. *Oedipina elongata* (Schmidt) from Guatemala and southern Mexico.

2. *Oedipina collaris* (Stejneger) a very large species from Nicaragua.

3. *Oedipina parvipes* (Peters) from Colombia. Also reported from Panamá.

4. *Oedipina complex* (Dunn) from Canal Zone.

From Costa Rica five species have been described, two of which are a part of the present collection. These are:

5. *Oedipina serpens* Taylor allied to *collaris*.

6. *Oedipina vermicularis* (Gray).

7. *Oedipina uniformis* Keferstein.

8. *Oedipina alfaroi* Dunn, perhaps allied to *elongata* (both are without maxillary teeth).

9. *Oedipina syndactyla* Taylor.

The collections from Costa Rica which are before me, contain 69 specimens of this genus, and they may be segregated as follows:

1. A large form from near Turrialba (2000 ft.) described as *Oedipina serpens* Taylor. One specimen.

2. A lowland form from the Pacific slope at San Isidro El General. One specimen.

3. A lowland form from Los Diamantes on the Caribbean slope. Fifty specimens.

4. A lowland form living with the preceding, having a slenderer body and smaller limbs. Five specimens.

5. A large form from near Turrialba 2000 ft. and Cervantes 4000+ ft. Five specimens.

6. An extremely-long-tailed species living with the preceding form at Cervantes. One specimen.

7. A form from approximately 6500 ft. elev. on Volcán Turrialba having a very unusual arrangement of the paravomerine teeth. One specimen.

8. A slender form with smooth elongate body; one specimen from Volcán Poás, described as *Oedipina syndactyla* Taylor.

9. Living with the preceding, a robust form generally resembling the Turrialba-Cervantes specimens but with the limbs greatly reduced. Five specimens.

Of the nine groups two have already been described (*serpens* and *syndactyla*); since none of the forms lack maxillary teeth none can be associated with *Oedipina alfaroi* Dunn.

There remain seven forms and two names, *Oedipina vermicularis* and *Oedipina uniformis*. Unfortunately both of these species are inadequately described so that the assignment of specimens to the names is not an easy task. The exact type localities of these named

species are unknown save that they are from "Costa Rica," and hence throw no light on the matter. The anatomical details given are few and may apply to more than a single form. On the basis of size both species exceed a snout-vent length of 50 millimeters. Since only three of the forms at hand seem to reach this size, it is most probable that only to these, if any, may the names be applicable. Two of these are forms occurring at Turrialba and Cervantes (Nos. 5 and 6 of the preceding list), and the third is the large form occurring on Volcán Poás (No. 9). Of these three, No. 5 would appear to agree most closely to *uniformis*, and to these I have assigned this name. I believe none of the forms are to be associated with *vermicularis*.

The following table of comparative measurements is given:

COMPARATIVE MEASUREMENTS OF OEDIPINA

	Uniformis*	Vermicularis	Volcan Poas (No. 9)	Volcan Poas (No. 9)	Turrialba (No. 5)	Cervantes (No. 5)	Cervantes (No. 6)
Total length	137	178	168	165 +	181 +	183	189.8
Snout to vent	51	54	52	57	56	52	49.8
Snout to foreleg	11	....	10.9	12	13	13.2	9.6
Axilla to groin	35		35	38	37	34.5	35
Tail length	86 +	124	116	108 +	125 +	131	140
Head length	5	6	7.6	8	8.6	9	6.5
Head width	4.5	3.5	4.2	5	5.4	5.3	4.3
Arm	(5)?	4	4	4.7	6.2	6	3.5
Leg	5	4.5	4.4	4.5	6.3	6.1	3.7
Head width in length	11.33	15.43	12.43	11.14	10.37	9.81	11.6
Costal groove	19	19	19.5	19.5	19	20	20

* Type measurements of *uniformis* and *vermicularis* as given, are arranged as nearly as possible to correspond to measurements here given for other forms. The tail is probably partly regenerated. In some cases the measurements represent close estimates.

A comparison of measurements shows certain differences between *Oedipina uniformis* and *Oedipina vermicularis*. The differences in measurements may or may not be significant since the technique of measurement of two workers may admittedly be different, but despite this possibility it would appear that the head is longer (20%) and narrower (22%) and the leg is shorter (10%) in a specimen that is nearly six percent longer from snout to vent. Moreover the tail in *O. vermicularis* is said to be "as thick as the body in its whole extent, rounded at the end." The type of *uniformis* has a head width of 4.5 mm., a body width of 4.5 mm. but the tail at its base is only 3 mm. The head width in snout-to-vent length in *uniformis* is 11.33 times; in *vermicularis*, 15.43 times. On the basis of these facts it would appear that there is insufficient evidence to warrant placing the forms in synonymy. The two types should both be examined and compared by a competent observer, and detailed

descriptions of the forms presented. Then and only then can there be certainty as to the proper usage of the two names.

Because of a closer approach of the large, central plateau form to the measurement of *uniformis* I am associating these specimens with that name. Other characters given in the type description (somewhat flattened head, cylindrical body, tail twice snout-vent length) all agree. The statement, "limbs light, almost without color" however does not agree completely. The limbs are distinctly lighter

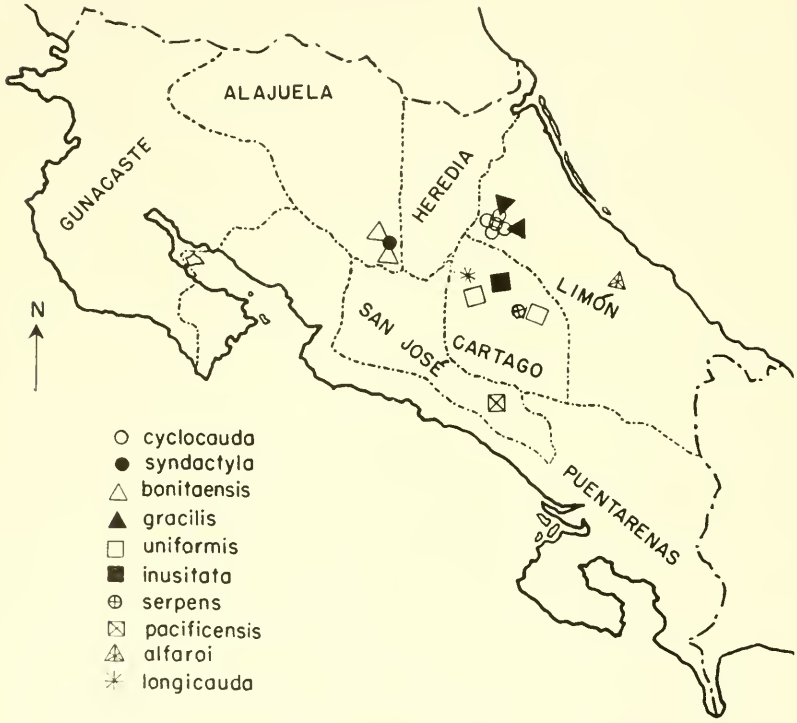

FIG. 5. Distribution of the species of *Oedipina* in Costa Rica.

than the body but do not approach the "without color" stage. That condition in the type might conceivably be due to fading. The apparent variation of the costal grooves may be due to method of counting the grooves.

The remaining forms are here treated as undescribed species. I am aware that this number of forms is large, and that larger collections may conceivably point to subspecific relations of certain of

those here named. The characters, where series are available, however, bespeak constancy.

A key has been devised as best showing the differential specific characteristics of the forms occurring in Costa Rica. It is applicable to the larger or largest adults known for each form.

KEY TO THE SPECIES OF THE GENUS OEDIPINA

1. Teeth absent in the maxilla; snout rather pointed; 20 costal grooves; one premaxillary tooth, not piercing lip, head width in length 12-14; folds between adpressed limbs 14-16; tail about twice snout-vent length. Panamá and southern Costa Rica ..... *alfaroi* Dunn

   Teeth present in maxilla; costal grooves 17-20 2

2. Smaller slender form under 65 mm. snout-to-vent length 4

   Large form: 70 mm. or more snout-vent length 3

3. Snout sharp (*fide* Dunn); 11 costal folds between adpressed limbs; black with lighter dorsal markings; 19 costal grooves; head width 7.5 times in snout-vent length; dark preocular spot, a narrow postocular black streak; skin granular; tail 2.6 times body length. Nicaragua to ?Panamá ..... *collaris* (Stejneger)

   Snout blunt, truncate, flattened; nearly uniform gray-slate; head width in snout-vent length 8.4 times; skin smooth; 9 costal folds between adpressed limbs; maxillary teeth 50-50. Eastern Costa Rica ..... *serpens* Taylor

4. Costal grooves 17 5

   Costal grooves 19-20 6

5. Digits terminate in rather sharp points; legs separated by 8 costal folds; head width in snout-vent length 9 times; snout sharp; eyes rather small; teeth on maxilla only to choanae; 25 maxillary teeth piercing gum; tail less than twice snout-vent length; brown above, light gray below. Colombia to Panamá, *parvipes* (Peters)

   Digits not sharp pointed; legs separated by 9 costal folds; snout short and blunt; head width in snout-vent length 7.5 times; brownish black with brown flecks; leaden below; tail less than twice snout-vent length; "maxillary completely toothed"; eye equal to its length from snout tip. Canal Zone .. *complex* (Dunn)

6. Paravomerine teeth in a single or double patch, more or less in a single plane 7

   Paravomerine tooth-patches posteriorly strongly deflected downward; a small pit on occiput; head width in snout-vent length 10.7; 44.2 mm. snout-venth length; tail 87 mm. Volcán Turrialba ..... *inusitata* Taylor

7. Head width in head-body length 15.4 times (Costa Rica) *vermicularis* (Gray)

   Head width in head-body length less than 13 times 8

8. Arm and leg in snout-vent length approximately 10 or less times, 9

   Arm and leg in snout-vent length 11 or more times 10

9. Greatest snout-vent length 46 mm. (50 specimens). Tail rarely reaching twice length of body, the average being approximately 1.9 times; maxillary teeth 16 to 20 on each side; 12.5 folds between limbs; snout rather pointed; tail nearly as wide body for much of its length, nearly cylindrical; arm in snout-vent length approximately 9 times; head width in same, 10.7 times; elevation approx. 1000 ft. northeastern Costa Rica ..... *cyclocauda* Taylor

Greatest known snout-vent length 61 mm.; tail 2.5 times head-body length; maxillary teeth 23 to 29; legs separated by 12 costal folds; snout rounded; tail tapering from base; elevation 2000-4000 ft.; arm in snout-vent length approximately 9 times; head width in same, 10 (-11) times. Central Plateau, Costa Rica ..... *uniformis* Keferstein

10. Larger forms 50-57 mm. snout-vent length 11

Smaller forms less than 50 mm. snout-vent length 13

11. Maxillary teeth reduced, 18 to 20; snout-vent length 49.8; tail much elongated, 2.8 times snout-vent length; 20 costal grooves; width of head in snout-vent length 11.6 times; arm in same, 14.2; 90 caudal grooves. Central Plateau, Costa Rica ..... *longissima* Taylor

Maxillary teeth increased, 24-29 12

12. Body proportionally longer, limbs slender; head width in snout-vent length 12.7 times; arm in same, 13.2 times; (tail?); maxillary teeth 27-29; mandibular teeth 33-36; south slope Volcán Poás, 7000 ft. ..... *syndactyla* Taylor

Body less slender, proportionally shorter; head width in snout-vent length (approx.) 12; arm in same, 13.4; maxillary teeth 24 to 28; mandibular teeth 31 to 35. South slope Volcán Poás, 6000 to 7000 ft., Costa Rica ..... *bonitaensis* Taylor

13. Without white markings on head; 20 costal grooves, maxillary teeth total 37-45; length 41.5 mm. ..... *gracilis* Taylor

A pair of light markings on head; maxillary teeth total 26; length 42.5 mm. ..... *pacificensis* Taylor

Oedipina serpens Taylor

Plate LXXXVI, fig. 1; text fig. 6

Oedipina serpens Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 1, Apr. 20, 1949, pp. 286-288 (type locality, Morehouse Finca, 5 mi. southwest Turrialba, Costa Rica, E. H. Taylor, coll. Erroneously stated "Morehead" Finca).

Diagnosis: A very large species of the genus; snout to end of vent, 74.5 mm.; tail more than twice head-body length; width of head in head-body length, 9.08 times; head length to gular fold

PLATE LXXXVI. Fig. 1. *Oedipina serpens* Taylor. Type, K.U.M.N.H. No. 23815, Morehouse Finca, 5 mi. SW Turrialba, Costa Rica. Total length of specimen 210.5 mm. Fig. 2. *Oedipina uniformis* Keferstein, K.U.M.N.H. No. 291, Cervantes, Costa Rica. Total length 183 mm. Fig. 3. *Oedipina bonitaensis* sp. nov. Type K.U.M.N.H. No. 647, 6 mi. by road, W of Isla Bonita, Volcán Poás, Costa Rica. Total length, 205 mm.

1 2 3

(median), 6.1 times; snout rather elongate, truncate not "sharp"; eye small; snout strongly overhanging lower jaw; digits grown together, free at tip, and rounded; 8-9 costal folds between adpressed limbs.

Description of the type: (K. U. M. N. H. No. 23815) Snout rather elongate, truncate, the dorsal surface curving without trace of canthus rostralis; median part of snout and interorbital region most elevated; eye very small, its diameter contained in snout length twice, or very slightly less; a small swelling below nostril on lip; posterior part of eyelids not tucked under a diagonal fold; nostrils very small, lunate in shape; width of upper eyelid in smallest interorbital distance, three times.

Gular fold strong, curving forward mesially; from sides of fold a nuchal groove runs up on side of neck but fails to meet its fellow on the mid-dorsal line; a distinct postorbital groove runs back from the eye directed slightly downward, then straight back to beginning of nuchal groove; a groove crosses chin in front of the gular fold, passes behind angle of mouth and reaches to dorsal surface of occiput; a short groove about midway between this and the nuchal groove laterally terminating at postorbital groove; only a faint suggestion of an arched groove on chin; no orbitolabial groove; no median dorsal groove; costal grooves nineteen, traceable to mid-ventral line, and to near middle of back; presumably a constriction at base of tail (tail severed); skin very smooth; limbs small, separated by nine costal folds when adpressed.

Arm adpressed reaches about two thirds distance to eye; fingers broad, grown together rather than "webbed", tips free with indistinct pads below; first finger without free tip, rather well developed; median finger rounded at tip; the other two fingers slightly narrowed at tip; toes very broad, grown together, the tips rounded, terminal joint free on all save inner, with small pads below tips; a white glandular spot behind leg insertion; walls of cloaca with very numerous papillae. Tail (severed and terminal portion missing) thick at base, tapering gradually; 52+ caudal grooves present.

Paravomerine teeth in two series narrowly separated mesially; vomerine teeth in two series, 15-16, which originate much outside outer level of choanae, run straight across mouth for greater part of their length, then curve back separated from each other by a distance equal to space between four teeth and separated from the paravomerine series by only a slightly greater distance. Choanae small, their length contained in distance between them about five times; three premaxillary teeth piercing gums; maxillary teeth about

50-50; mandibular teeth about 55-55; a strong free sublingual fold. Posterior extension of epibranchial reaches back to level of arm insertion.

Color: Dorsal and ventral color, grayish slate (under a lens the circular glands are whitish gray, the intervening space black); spots behind leg insertion bluish white; under surface of limbs somewhat brownish with some small whitish flecks; tip of snout with some indefinite lighter flecks; subnarial swellings and a minute line on

FIG. 6. *Oedipina serpens.* Type. Upper. Left hand, dorsal and ventral views. Lower. Left foot, dorsal and ventral views.

edge of upper lip cream; lower eyelid and part of edge of upper eyelid whitish; medial area on chin brownish with creamy flecks; hands and feet grayish on palms and soles.

Measurements in mm.: Snout to posterior end of vent, 74.5; snout to arm insertion, 20; axilla to groin, 47; arm, 10; leg, 13.2; head width, 8.8; head length to gular fold (medial), 12; head length to nuchal fold (lateral), 15; width of body, 9; width of tail base, 7; length of tail, 136 (missing part estimated at about 50 mm.).

Remarks: The specimen was found under a log in rather soft mud at the edge of a stream bank. It was especially active and elusive and escaped into a pile of large chips from which it was recaptured

with considerable effort. The tail was broken and part lost, perhaps by my stepping on chips under which it was moving. Search was made for the lost portion of the tail but it was not found.

Relationship: The relationship apparently is with *Oedipina collaris* Stejneger. The following table of contrasting characters shows the major differences between *collaris* and the one here described.

Oedipina collaris	*Oedipina serpens*
1. Snout sharp.	1. Snout blunt, strongly truncate.
2. Head width in head body length, 7.5 times.	2. Head width in head-body length, 8.4 times.
3. Head length in head body length, 4.5 times.	3. Head length in head-body length, 4.9—6.2 times.*
4. Skin granular.	4. Skin smooth.
5. Vomerine teeth about nine.	5. Vomerine teeth fifteen.
6. Vomerine teeth extend straight across mouth.	6. Vomerine teeth straight for part of series then curving back.
7. Fingers and toes short, scarcely flattened.	7. Fingers and toes long, strongly flattened.
8. Paravomerine (parasphenoid) teeth separated from vomerine teeth by half length of latter series.	8. Paravomerine teeth separated from vomerine teeth by one third length of one of latter series.
9. Eleven costal folds between adpressed limbs.	9. Nine costal folds between adpressed limbs.
10. Last joint of the third and fourth toes free of membrane.	10. Last joints of second, third and fourth free of membrane.
11. Large dark preocular spot and a narrow black postocular streak.	11. These markings not present.

Oedipina uniformis Keferstein †

Plate LXXXVI, fig. 2; text fig. 7

Oedipina uniformis Keferstein, Nachricht. Ges. Wiss. Göttingen, 1868, p. 331 (type locality, Costa Rica; von Seebach, coll.); Archiv. für Naturg., Jahrg. 34, vol. 1, 1868, p. 299, pl. 9, figs. 8, 9; Günther, Zool. Record for 1868, (Gives Aug. 1868 as the date of publication of Keferstein's *Oedipina uniformis* and Oct. 1868 for Gray's *Ophiobatrachus vermicularis* which Günther says is "evidently the same animal"); Dunn, Bull. Mus. Comp. Zool., vol. 62, 1918, p. 471; ?Noble, Bull. Amer. Mus. Nat. Hist., vol. 44, 1921, p. 2 (skull); Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 1, May 15, 1944, pp. 226-227.

Spelerpes uniformis Strauch, Mem. Acad. Sci., St. Petersbourg, ser. 7, vol. 16, pt. 4, p. 84; Boulenger, Catalogue of the Batrachia Gradientia s. Caudata and Batrachia Apoda in the collection of the British Museum, Ed. 2, 1882, p. 75 (*part.*) (only type of *vermicularis* mentioned from Costa Rica); Günther, Biologia Centrali-Americana, Jan. 1902, p. 304 (Costa Rican localities: La Palma, alt. 1600 m., Biolly coll.; Bebedero and Irazú, Underwood coll.).

Oedipus uniformis Dunn, Zool. Ser. Field Mus. Nat. Hist., vol. 12, 1924, p. 99; The Salamanders of the Family Plethodontidae, Smith College Publ., 1926, pp. 427-430 (*part.*).

* The gular folds curves strongly forward on middle of throat; head measured to this point, its length is 12 mm., to the side of head the measurement is 15 mm.

† Certain of these references may actually apply to other forms.

Description of species: K.U.M.N.H. No. 29975 ♂, Cervantes, Costa Rica, elevation somewhat above 4000 ft., July 9, 1947, E. H. Taylor and R. C. Taylor colls.). Head a somewhat truncate oval; eyes small, the length of eye opening (1.85 mm.) slightly smaller than snout length (1.9 mm.); top of head flattened to base of snout, then curving down slightly to nostrils which are nearly terminal; groove from nostril running back and down, the subnarial swelling distinctly behind the posterior level of nostril; groove following inner edge of upper eyelids continued behind eye, as the postorbital groove, to the lateral nuchal groove, the groove curving down strongly, forming an angle; a somewhat sinuous groove begins on side of occiput, bisects the postorbital groove, continues down across the chin to opposite side; on middle part of chin it curves back slightly and a pair of grooves run forward on chin completing an arch; a small groove from angle of mouth runs back and bisects the groove on side of head. A prominent gular groove and fold curves forward on neck; from its side a lateral nuchal groove curves forward and upward but fails distinctly to meet its fellow from opposite side.

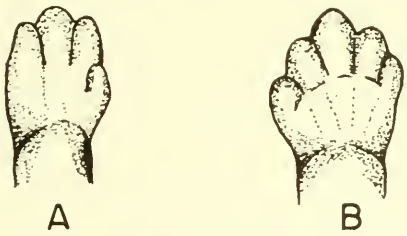

FIG. 7. *Oedipina uniformis.* A. Left hand, dorsal view, B. Right foot, dorsal view. (Much enlarged.)

Tongue free with a distinct sublingual fold; 24-26 maxillary teeth; two premaxillary teeth; mandibular teeth 25-27; choana rather large followed by a postchoanal groove that is nearly the width of choana; vomerine teeth in two strongly elevated rows beginning beyond outer level of choanae, curving in and back, 10 teeth in each series, separated mesially by a distance approximately equal to a diastema between two teeth; palate in front of vomerine ridges rather shallow with a median shallow pit; behind ridges there are deep excavations leaving the elevation of the ridges .85 mm. high; paravomerine teeth in a single group, pointed anteriorly, widened posteriorly and rounded behind; a mesial area near middle of patch

without teeth; total number of paravomerine teeth approximately 127.

Costal grooves 20 (the posterior costal fold partly divided, the groove not reaching lower level of other grooves); 80 or 81 caudal grooves present behind vent, the tail not certainly constricted at base; no dorsal longitudinal median groove on body or tail, no groove on underside of tail; arm short, hand slender, palmate, four fingers present, grown together with the tips of the second and third free, rather pointed; outer fingers completely involved; leg short, slender, the foot palmate, the limbs when adpressed separated by the equivalent of 12 costal folds.

Color: Dorsal and ventral color above deep bluish slate; the head (submerged) is brownish; the limbs lighter brownish-flesh with a fine darker reticulum; palm and sole lacking pigment; gray-white postiliac spot and an indistinct light area about insertion of arm and leg; outer edge of chin lighter then central part which in turn is a little lighter than venter; an area on top of head in which the individual skin glands are more distinct than elsewhere; subnarial swelling and medial area of upper lip light.

Measurements in mm.: The measurements of this specimen are included in the table of measurements for this species.

TABLE OF MEASUREMENTS AND DATA ON OEDIPINA UNIFORMIS

MUSEUM	RCT	KUMNH	RCT	RCT	KUMNH
Number	1021–A	29975	290	222	29976
Sex	♂	♂	♀	♂	♂
Locality	Cer-vantes	Cer-vantes	Cer-vantes	Turri-alba	Turri-alba
Snout to vent (body length)	56	52	50.4	54	44
Snout to foreleg	13	13.2	12	12	10.5
Axilla to groin	37	34.5	32.5	35	28.6
Length to gular fold (head length)	8.6	9	8	8	7.4
Width of head	5.4	5.3	5.5	5.3	4.5
Tail length	125+	131	89+	110+	61+
Arm	6.2	6	5.8	6.15	5
Leg	6.3	1	6.1	6	5.5
Head width in body	10.37	9.8	9.1	10.1	9.8
Head length in body	6.51	5.8	6.3	6.75	5.9
Costal grooves	19	20	19	19	20
Costal folds	18	19	18	18	19
Caudal folds	68+	80	55+	?	50
Maxillary teeth	24–26	23–26	25–26	29–26	20–19
Mandibular teeth	25–27	26–28	34–36	23–25	33–33
Premaxillary teeth	4	2	5	3	3
Vomerine teeth	10–12	8–8	11–11	10–10	6–6
Paravomerine teeth	127	140	140	?	?

Variation: The head of this form is definitely brownish and there is in some of the specimens a suggestion of brown on the dorsal surface; this is due to the color of the skin-glands which under a lens

may be seen as minute rounded areas surrounded by a blackish reticulum. The brown on the head is more definite in a younger specimen (R.C.T. No. 290); the underside of the hind limbs in R.C.T. No. 1021-A is lighter than in other specimens. The anal slit in all the specimens, except No. 29975, is light. In all, there is a sharply-defined white line in the gular groove, but hidden by the gular fold.

Males have the cloacal walls very finely papillate, but in the females indistinct folds are present. Males have the submental hedonic gland very irregularly shaped, not prominent.

The tails of Nos. 29975, 222 and 29976 are complete; that of R.C.T. No. 222 has the terminal part regenerating. The tip is missing in 102-A, a part estimated at 12 mm.

Oedipina vermicularis (Gray)

Ophiobatrachus vermicularis Gray, Ann. Mag. Nat. Hist., ser. 4, vol. 2, 1868 (Oct.), p. 298 (type locality, Costa Rica).

Opheobatrachus vermicularis Cope, Proc. Acad. Nat. Sci. Philadelphia, 1869, p. 102 (At this time Cope believed Gray's name had been published before Keferstein's, and placed *Oedipina uniformis* in synonomy.); Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 8, 1875, p. 96 (*part.*?) (very probably two species are represented in the lot. He reports one specimen from Pico Blanco 6000 ft., and two from eastern lowland Costa Rica).

Spelerpes vermicularis Smith, The Tailed Amphibia, 1877, p. 94; ?Brocchi, Étude sur les Batraciens; Mission Scientifique au Mexique et dans l'Amérique Centrale, livr. 3, 1883, p. 118, pl. 20, fig. 1, (*part.*) (Costa Rica and Guatemala). The figure given is of a specimen from Guatemala and most probably belongs to another species.

Spelerpes uniformis Boulenger (*part.*), Catalogue of the Batrachia Gradientia s. Caudata, and Batrachia Apoda in the Collection of the British Museum, 2nd ed., 1882, p. 75 (gives measurements of the type of *vermicularis*).

Description of species: The original description offers but little information on this form. The differences in measurements from those of *uniformis* (as given by Boulenger, *loc cit.*) give evidence that it is not a synonym of *uniformis*. Thus the length of the leg in snout-to-vent length in *uniformis* is approximately 10 times; in *vermicularis* approximately 12 times; the head width of *uniformis* in snout-to-vent length is approximately 11.1 times; in *vermicularis* 15.4 times; the head length of the two forms in snout-to-vent length is respectively 10.4 and 9 times. It will thus be seen that *vermicularis* has a long body, and a very narrow elongate head.

The data available on the type as given by Boulenger, *loc. cit.*, is as follows:

"Parasphenoid [= paravomerine] teeth in a single patch. Habit

more worm-like still [than *Spelerpes lineolus*]. Tail as thick as the body in its whole extent, rounded at end. Nineteen costal grooves."

Total length	178	mm.
Snout to vent	54	mm.
Head [length]	6	mm.
Width of head	3½	mm.
Fore limb	4	mm.
Hind limb	4½	mm.
Tail	124	mm.

The above measurements obviously are those of the type. With the publication of a careful, detailed description of this species, together with accurate measurements, it may be possible to refer to it one of the forms here described as new.

Oedipina bonitaensis sp. nov.

Plate LXXXVI, fig. 3; text fig. 8

Type: Kansas University Museum of Natural History No. 29972 ♀ collected approximately 6 mi. (by road) west of Isla Bonita (American Cinchona Plantation), southern slope of Volcán Poás, Costa Rica; Aug. 3, 1947. R. C. Taylor and E. H. Taylor colls.

Paratypes: R.C.T. Nos. 645, 646, 649; K.U.M.N.H. Nos. 29973, 29974; same locality data, and collectors.

Diagnosis: A medium-large *Oedipina*, the largest known snout-to-end of vent measurement, 57 mm.; width of head in snout-vent length, 11.2 times; adpressed limbs separated by 14 costal folds; length of eye greater than axial snout length; tail length 2.7 times snout-to-vent length; maxillary teeth 24-28; palatal area, in front of vomerine ridges, on a level with palate behind them.

Description of type (♀): Head as wide or slightly wider than body; the length of the eye (1.8 mm.) greater than axial length of the snout (1.45 mm.); snout extending beyond lip .7 mm.; groove from small nostril runs diagonally to the subnarial swelling which is behind, but reaching posterior level of, the nostril; posterior part of eyelids terminate in a short groove; occipital and interorbital region flat, the top of the snout very slightly elevated and in profile rounding forward to lip; no canthus; groove bordering inner edge of supraorbital part of eyelid scarcely indicated; a vertical groove begins near top level of occiput, runs down across jaws curving backward as it crosses chin; on each side from outer ends of the curved part two distinct grooves run forward on chin but fail to meet by a considerable distance; gular fold strong, curving forward on throat, and from its ends, a nuchal groove arises, curves back a little,

then upwards and forward, meeting its fellow on the mid-dorsal line; elevation caused by the epibranchial cartilage can be traced but little beyond hind level of arm insertion, postorbital groove from orbit runs diagonally back until it bisects the vertical groove then continues back horizontally to end of gular fold.

Maxillary teeth 26-26, running back to posterior level of eye; one or two premaxillary teeth piercing the gum; vomerine teeth beginning beyond outer level of the choanae, but failing to meet mesially by a diastema half diameter of a choanae, separated from paravomerine teeth by a distance more than twice diameter of a choana; paravomerine tooth series forming a patch more or less completely divided mesially by a distinct line without teeth, the teeth totaling approximately 185; mandibular teeth approximately 35-35; a distinct sublingual fold present.

Arm short, small, when adpressed covering two and one-fourth costal folds; outer fingers completely involved in the palm; second

FIG. 8. *Oedipina bonitaensis*. Type. A. Right hand, dorsal view. B. Right foot, dorsal view. (Much enlarged.)

with tip, third with about one and a half phalanges free, the two digits closely approximated but with a slight emargination between; outer toes involved in the sole, three inner digits with the tips free, the digits closely grown together save for a slight emargination (the right foot is abnormal, having only four digits); 20 costal grooves, counting one in the groin. The large costal fold in front of the hind leg is only partially divided, the number of costal folds is properly 18½ since a part of the 19th is actually above the hind limb; 85 caudal folds, the tail subcylindrical and tapering, with a growing tip; a glandular area behind leg insertion; cloacal walls papillate; skin generally smooth although pits are visible under magnification.

Color: Body and head brownish, the sides gray or slaty brown; the ventral surfaces from gular fold to vent lighter than dorsum; chin and throat much lighter than venter; tail slate or bluish slate,

not or but scarcely lighter below; a white spot covers the postiliac gland behind leg insertion; limbs on dorsal parts nearly as dark as dorsum; undersides lighter with some small whitish marks; chin with some indefinite whitish areas or reticulations; edge of upper eyelids dull cream.

Measurements: (See table).

Remarks: There are two young specimens taken at the same time that are not included in the table of data. They agree in such characters as their size and age would permit. Thus the tooth totals are smaller and the caudal folds fewer. All six specimens were taken from five to six miles west, by road, from Isla Bonita.

This species was found under logs. One other species, *Oedipina syndactyla* was taken in the general vicinity. This latter differs in having a smoother body surface; the grooves less distinct, proportionally greater snout-to-vent length in proportion to head width, much more slender body, more pointed snout, longer narrower digits, etc. These two forms should not be mistaken.

MEASUREMENTS AND DATA ON OEDIPINA BONITAENSIS SP. NOV.

MUSEUM	KUMNH	RCT	KUMNH	RCT
Number	29973	646	29974	645
Sex	♂	♀	♂	♂
Snout-to-vent (body length)	57	57	56	52
Snout to foreleg	12	11.4	11.6	10.9
Axilla to groin	38	39	37.9	35
Length to gular fold (head length)	8	8	8	7.6
Snout to lateral nuchal groove	9.1	9	9.1	9
Width of head	5	4.7	4.9	4.2
Tail length	108 +	136	149	116
Arm	4.7	4.3	4.2	4
Leg	4.5	4.5	4.6	4.4
Head width in body length	11.14	12.1	11.4	12.2
Head length in body length	7.1	7.1	7	6.8
Costal grooves	20	20	20	20
Costal folds	18½	18½	18½	18½
Caudal	54 +	91	85 +	78 +
Maxillary teeth	28–27	25–24	26–26	26–25
Mandibular teeth	32–32	35–35	32–31	31–31
Vomerine teeth	9–9	12–12	11–10	10–9
Paravomerine teeth	180			

Oedipina cyclocauda sp. nov.

Plate LXXXVII, fig. 4; text fig. 9

Type: Kansas University Museum of Natural History No. 25066, collected at Los Diamantes (1 mile south of Gúapiles), Costa Rica, September 1-8, 1947, by Richard C. Taylor and Edward H. Taylor.

Paratypes: K. U. M. N. H. Nos. 25038-25065; RCT field Nos. 3137-3176, same locality data, and collectors.

Diagnosis: A small species of the genus, maximum known length from snout to end of vent, 46 mm.; tail 1.9 to approximately 2

times head-body length; head not distinctly wider than body; tail nearly half its length maintaining a width closely approaching that of body; adpressed limbs of large adults separated by approximately 12.5 costal folds; head width in snout-vent length, approximately 11 times; tongue rather far forward, with a distinct sublingual fold; maxillary teeth 16 to 20 on each side; anterior part of palate not elevated more than that part posterior to vomerine teeth; vomerine tooth series straight across palate to near median line where they turn back suddenly; paravomerine teeth all on same level; 19 costal grooves; snout narrowed toward tip.

Description of the type: Body and tail for the most part cylindrical, the tail for much of its length very little narrower than body; snout somewhat pointed, rather than blunt; the eyes small; the length of eye (edge of upper eyelid) equal to or slightly less than length of snout; width of an upper eyelid 1.8 times in interorbital distance. Nostril small, the groove running down and only slightly backwards to the subnarial swelling whose anterior edge is below edge of nostril; groove from eyelid running diagonally back and down from eye, then straight back to nuchal groove, bisecting a groove beginning at upper surface of head and running across jaw and throat, becoming somewhat concave mesially on chin; from this, two narrow, slightly-converging grooves run forward on chin; nuchal fold not strong, curving slightly forward on throat, the nuchal groove passing up on sides of neck but failing to reach middorsal line; top of head smooth, somewhat rounded across occiput without any area of glandular pits evident; in lateral profile snout tip is farther forward than lip; tongue rather far forward with a sublingual fold; maxillary teeth 19-20, bearing brownish tips; premaxillary teeth (♂), two, piercing the inner edge of lip, not visible externally; vomerine teeth 9-10 on two elevated ridges, nearly transverse save that the inner ends of the two series curve back; paravomerine teeth approximately 180, all on same plane, in a single patch, not, or but indefinitely notched behind, separated from the vomerine teeth by a space less than half length of one vomerine series; width of patch, twice in its length. Four fingers on hand, inner small (abnormally rudimentary on right hand), third longest, its tip free as is that of second; five toes, all somewhat pointed at tips; third longest, second and fourth subequal, tips of all three free for nearly a third of their length; tip of fourth minutely free; adpressed limbs separated by 12.3 costal folds. Costal grooves 19, last one indicated a short distance in front of groin; a well-defined postiliac gland; cloaca lined anteriorly with

papilla in male (folds in female). Skin smooth throughout body and tail; under a lens, skin glands usually not visible on head, dorsum, or on upper part of sides; skin glands visible low on sides, less so on chin, venter and on lateral and ventral surfaces of tail; caudal grooves 68, more or less clearly marked.

Measurements in mm.: Snout to end of vent 44.6; snout to arm insertion 10; axilla to groin 28.8; tail 95, width of head 4.1; width of body 4.2; width of tail at base 4; length of head (to middle of nuchal fold) 7; head to nuchal groove (lateral) 7.9; arm length 4.9; leg length 5.2; hand width 1; foot width 1.3.

Color: Dorsally and laterally on head, body, and tail, grayish slate, becoming slightly brownish on latter half of tail; chin dirty gray-brown with some lighter areas; nuchal fold cream; arms and legs lighter below than on dorsal surfaces; a cream cloacal spot,

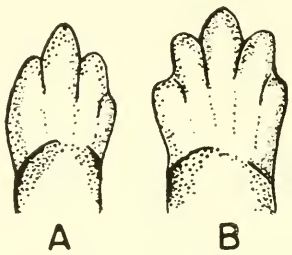

FIG. 9. *Oedipina cyclocauda.* Type. A. left hand, dorsal view. B. Right foot, dorsal view. (Much enlarged.)

and a whitish spot covering postfemoral gland; narrow, indistinct lighter areas bordering insertion of limbs.

Variation: The accompanying table for the most part shows a relatively small amount of significant variation. The counts of the paravomerine and other teeth are close approximations, usually counting spaces where teeth are missing.

A young specimen (35 mm. snout-to-vent) has the following dental counts: maxillary 15-16; vomerine 10-8; mandibular 25-25; approximately 160 paravomerine teeth. Thus the normal number of teeth are acquired early in life; however the aggregate is a little larger in old adults.

The glands of the skin on dorsal and lateral regions are visible in many specimens, although they are not visible on all parts of the type. The number of caudal folds of grooves varied, in the measured series, from about 56 to 70; in these the distinctness of the

PLATE LXXXVII. Fig. 1. *Oedipina syndactyla* Taylor. Type, K.U.M.N.H. No. 29962, 4 mi. W by road from Isla Bonita, Volcán Poás, Costa Rica. Snout to vent length, 54.8 mm. Fig. 2. *Oedipina pacificensis* sp. nov. Type, K.U.M.N.H. No. 29965, 2 mi. E San Isidro El General. Total length, 119.5 mm. Fig. 3. *Oedipina inusitata* sp. nov. Type, K.U.M.N.H. No. 29964, 3 mi. NE Santa Cruz, Volcán Turrialba. Total length, 133 mm. Fig. 4. *Oedipina cyclocauda* sp. nov. Type, K.U.M.N.H. No. 25066, Los Diamantes, 1 mile S Guápiles, Costa Rica. Total length, 139.6 mm. Fig. 5. *Oedipina longissima* sp. nov. Type, K.U.M.N.H. No. 29963, Cervantes, Costa Rica. Total length, 188.9 mm.

vertebral differentiation of the tip of the tail varied. In some, the grooves were not indicated and the number of vertebrae were not estimated in these. The tail length reaches to 2.2 times snout-vent length (in No. 3158 ♂), but in most cases the tail is about twice the head-body length. The tail in the younger specimens is usually a little narrower in relation to the width of the body than in the type.

Remarks: These specimens were taken largely from rotting logs in which beetle larvae had burrowed. The salamanders seemed to follow the tunnels made by the departed larvae. Another species, *Oedipina gracilis*, occurred in the same logs. Other specimens were found in piles of rotting weeds or about stumps. They moved rapidly and often escaped after being exposed by chopping the logs to pieces. Numerous specimens were destroyed in the chopping process.

The name given is in reference to the circular caudal grooves.

Oedipina syndactyla Taylor

Plate LXXXVII, fig. 1; text fig. 10

Oedipina syndactyla Taylor, Proc. Biol. Soc. Washington, vol. 61, Nov. 12, 1948, pp. 179-180 (type locality, 7000 ft. elev., 4 mi. W by road from Isla Bonita [American Cinchona Plantation], Volcán Poás, Costa Rica, Aug. 5, 1947. E. H. Taylor coll.).

Diagnosis: Snout bluntly pointed; body slender slightly angulate rather than cylindrical; eye large, longer than snout, equal to its distance from tip; 20 costal grooves; adpressed limbs separated by 14-15 costal folds; digits fused together rather than webbed, the digits elongate; the extreme tips of 2 fingers on hands, and 3 toes on feet, free; 27-29 maxillary teeth; 4 premaxillary teeth; 10-11 vomerine teeth; paravomerine teeth in two distinct elongate patches closely approximated; the toes relatively longer than in other *Oedipina*.

Description, from type: (K.U.M.N.H. No. 29962, field No. 843). Head moderately elongate, narrow, rather bluntly pointed, its width in snout-to-vent length 12.7 times; nostrils distinctly back from snout tip; eye large, its length greater than snout length, equal to its distance from tip; distance between nostrils equal to their distance from eye; eyelids approximately as wide as interorbital distance, not tucked under a fold posteriorly; a strong, curved, gular fold, from the sides of which emerges a nuchal groove that curves up on sides of head to dorsal surface; a vertical groove between eye and nuchal groove that crosses chin; a pair of grooves run forward from this but fail to form a complete arch on chin; a very dim groove

TABLE OF MEASUREMENTS (IN MM.), AND DATA FROM PARATYPE SERIES OF OEDIPINA CYCLOCAUDA

MUSEUM	RCT	KUMNH	RCT	RCT	RCT	RCT	RCT	RCT	RCT
Number	3145	25066	3162	3147	3138	3152	3140	3154	3158
Sex	♀	♂	♀	♀	♀	♂	♀	♂	♂
Snout to end of vent	46	44.6	44	43	42.6	42.6	41.6	41.2	41
Snout to foreleg	9.8	10	9.4	9	9.2	9.5	8.7	9	8.9
Snout to nuchal groove	8	7.9	8.1	7.8	7.7	7.3	7.2	7.6	7.9
Snout to nuchal fold	7	7	7	7	7	6.7	6.8	7	7
Axilla to groin	30.6	28.8	29	28	28.5	27.2	27	27.2	26.8
Head width	4.3	4.1	4.6	4.15	4.3	4.3	4	4	4.2
Tail length	82	95	74	69+	.....	76	75	76	90.3
Head length to nuchal fold	7	7	7	7	7	6.7	6.8	7	7
Arm	4.6	4.9	4.3	5	4.2	4.3	4.3	4.4	4.4
Leg	5.2	5.2	5.2	5.2	4.95	5	5.2	5	5.2
Costal grooves	19	19	19	19	19	19	19	19	19
Costal folds	18	18	18	18	18	18	18	18	18
Maxillary teeth	16–18	19–20	0–18	18–18	16–18	14–15	19–19	18–20	15–16
Mandibular teeth	23–24	25–25	28–28	27–27	26–26	26–25	27–27	26–28	23–23
Vomerine teeth	10–10	9–10	10–11	10–9	9–9	7–7	8–9	9–11	8–7
Paravomerine teeth	152	180	174	160	156	172	170	172	150
Premaxillary	4	1	4	4	4	3	4	2	3

from eye to the lateral nuchal groove; no groove on the inner border of upper eyelid.

A well-defined sublingual fold; 27-29 maxillary teeth (counting missing teeth), reaching slightly farther back than middle of eye; vomerine teeth 11-10, on ridges beginning outside level of choanae passing mesially for a distance, then turning back toward mesial line but narrowly separated mesially; 4 premaxillary teeth in the line of maxillary tooth row; 33-36 mandibular teeth; tongue free; paravomerine teeth in two elongate patches more or less contiguous anteriorly, separated from vomerine teeth by twice diameter of choana, the teeth numbering approximately 161 (new teeth are added on the outer edges; sometimes an elevation is present but the tooth had not erupted).

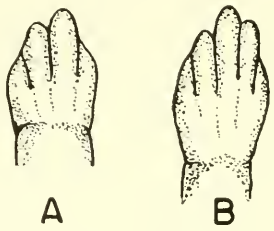

FIG. 10. *Oedipina syndactyla.* Type. A. Right hand, dorsal view. B. Left foot, dorsal view. (Much enlarged.)

Arms short, when extended along body their length equal to about 2½ folds; legs about same size; hands and feet small; digits rather elongate, narrow, grown together without emargination, tips of two middle fingers and three middle toes equally free, bluntly pointed; outer digits small, completely fused with adjoining digit and incorporated in foot or palm.

Skin very smooth, even under a lens the openings of the glands not or scarcely discernible (except for a specialized somewhat depressed diamond-shaped occipital area reaching to between eyes in which pits and the glands are especially distinct); 20 costal grooves or lines, indistinct, the costal folds not elevated; tail presumably with a basal constriction (tail severed immediately behind vent, the broken part short, partially regenerated); cloacal walls smooth with indications of lateral folds (female); a postiliac gland; a small elongate ridge preceding vent to between legs.

Color: Slate-gray above, gray below; edge of gular fold cream; chin much lighter than venter; a cream spot below insertion of arms

and legs; undersurface of upper arm and leg with cream markings; lower eyelid somewhat cream, and a lighter line following the nasolabial groove from nostril to lip. A light area about vent.

Measurements in mm.: Snout to end of vent, 54.8; tail short, with terminal regenerating portion broken off immediately behind vent; width of head, 4.3; length to median part of gular fold, 7.5; axilla to groin, 38; snout to arm insertion, 10.6; head width in snout-to-vent length, 12.7 times; head length in same, 7.3 times.

Remarks: The unique specimen was captured in more or less open pasture land at an elevation of about 7000 feet on Volcán Poás.

Another species, *Oedipina bonitaensis,* was found in the same general area about one to two miles farther west at about the same elevation, 6000-7000 feet. This form is larger, with a proportionally thicker head and body, the skin less shiny smooth, with proportionally thicker, shorter digits. The costal grooves are definitely grooves rather than lines; the snout is more rounded at the tip. Since the tail is incomplete in *syndactyla,* this character cannot be compared.

Oedipina longissima sp. nov.

Plate LXXXVII, fig. 5; text fig. 11

Type: Kansas University Museum of Natural History No. 29963 ♀, collected at Cervantes, Costa Rica, July 9, 1947, by Edward H. Taylor and Richard C. Taylor.

Diagnosis: A species of medium size, the snout-vent measurement 49.8 mm.; the tail 140 mm., two and eight-tenths times the snout-vent length; eye a little longer than snout; 20 costal grooves; caudal grooves 90; width of head (4.3 mm.) in snout-vent length, 11.6 times; head length (6.5 mm.) in same, 7.6 times; skull well ossified; no special pit or depression behind occiput; paravomerine teeth all on same level; maxillary teeth 20-18; adpressed limbs separated by about 14.5 costal folds; tongue far forward in mouth with a very well-developed sublingual fold; choanae small; tail subcircular, slightly compressed toward tip.

Description of type: A slender, elongated species, the tail 2.8 times the length from snout to end of vent; the head width (4.3 mm.) in snout-vent length (49.8 mm.), 11.6 times; head length (6.5 mm. from tip of snout to middle of nuchal fold) in same, 7.6 times; head rather flattened, rounding above, the eye small, the length of eye (free edge of lid) slightly longer than snout; snout moderately blunt, slightly emarginate medially seen from above; groove from nostril runs backward and downward; little or

no subnarial swelling; loreal region inflated so the surface across snout from lip to lip is a continuous curve; no groove marks the inner edge of eyelid; a strong groove from eye back to the nuchal fold, in nearly a straight line, bisecting a vertical groove that begins near top of head and crosses jaw to side of chin where it terminates; from near the ventral ends two fine grooves converging somewhat, run forward to near tip of chin. The nuchal groove with an ample fold, curving forward across the throat; on the sides the groove can be traced to near the median dorsal line; posterior extension of epibranchial forms fold that reaches to the second costal fold; width of an eyelid in interorbital width approximately two times. Tongue very far forward, with a strongly-developed sublingual fold; maxillary teeth 20-18; premaxillary teeth 4; vomerine teeth 8-10, in a very irregular row on two elevated ridges begin-

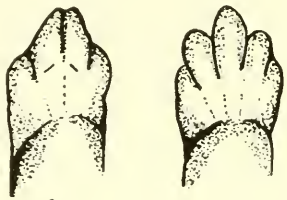

FIG. 11. *Oedipina longissima.* Type. A. Right hand, dorsal view. B. Right foot, dorsal view. (Much enlarged.)

ning outside of level of choanae and curving in and back, nearly meeting medially; paravomerine teeth approximately 150, in a large single patch all on the same level, rather narrowly separated from vomerine series; the patch is slightly notched behind, its greatest width in its greatest length 2.4 times; mandibular teeth 18-18; choanae small, the diameter of one in distance between them nearly four times; arm small, slender, width of hand .6 mm.; adpressed limbs separated by 14.5 costal folds; four fingers, the tips of three outer free; third longest, and bluntly pointed rather than rounded; leg (3.7 mm.) minutely longer than arm (3.5 mm.); five toes, the three inner largest, and free for nearly half their length, rounding at tips; first and fifth toes reduced, tips not free. A slightly elevated pitted area on the top of head extending forward between eyes; remainder of head smooth; body smooth or relatively so; tail without a basal constriction, subcircular in cross-section save

toward tip where it is slightly compressed laterally; caudal grooves 90 +; a rather large postiliac gland; under a lens glands visible over the body appearing as rounded cream spots in a brownish reticulum.

Measurements in mm.: Snout to vent 48.9; tail 140; snout to foreleg 9.6; snout to nuchal groove (lateral) 7.8; axilla to groin, 35; length of head 6.5; width of head 4.3; arm 3.5; leg 3.7.

Color: Head somewhat brownish, most distinctly brown over the dorsal pitted area; dorsal and lateral surface brownish with a suggestion of a grayish film; sides a little darker, dorsum and sides of tail bluish slate. Chin lighter than venter with a few lighter flecks scattered along sides of venter; underside of tail somewhat brownish, but lacking cream flecks.

Remarks: It is probable that this species has a larger number of caudal vertebrae (90 +) in old adults than any other plethodontid. The number increases throughout life or at least during the early years.

The most important distinguishing characters are: great tail length, the forward position of the tongue, and the discontinuity of the groove across chin.

The specimen was dislodged from loose soil under a rock.

Oedipina gracilis sp. nov.

Type: Kansas University Museum of Natural History No. 29969 ♂, collected at Los Diamantes, one mile south of Guápiles, Costa Rica, Sept. 8, 1947, by Richard C. Taylor and Edward H. Taylor.

Paratypes: K. U. M. N. H. Nos. 29968, 29970; R. C. T. Nos. 1420, 1419, topotypes, same collectors.

Diagnosis: A small species with much reduced limbs and an elongate tail; 19 costal folds, 20 costal grooves distinct; 86 caudal folds; body somewhat flattened, the tail cylindrical, tapering; eye large, longer than snout; maxillary teeth 18-19; vomerine teeth 7-7; the ridges not especially high; 2 premaxillary teeth piercing gum, limbs separated by 14 costal folds.

Description of the type: Snout-to-end-of-vent length, 41 mm.; width of head (4 mm.) in snout-vent length, 10.2 times; top of head flat, the snout rounded in profile, curving back to lip; tip of snout extending .8 mm. beyond lip; nostrils small, the nasal groove directed back and down to the subnarial swelling which is much behind posterior level of nostril; seen from above, snout rounded; interorbital width slightly greater than width of an eyelid; length of eye (1.7 mm.) greater than axial length of snout (1.25 mm.); a

groove, bordering inner edge of eyelids, continuous with the postorbital groove, which continues back to the nuchal groove, forming an angle where it touches the vertical groove; latter crosses jaw, straight on the sides, but curves back mesially; from this a pair of converging grooves run forward to near tip of chin, but fail to meet; a strong gular fold curves forward across neck, and a short distance up on the sides of neck; from its ends emerges the nuchal groove which curves back then runs up and somewhat forward on the neck to meet its fellow on the median line; a small vertical groove above the median posterior part of the postorbital groove; a groove from mouth angle reaches the first vertical groove; maxillary teeth 19-18; 2 premaxillary teeth piercing the gum; vomerine teeth in two series, on rather thick ridges beginning outside outer level of choanae, curving in and back, separated mesially by a space equal to diastema between two teeth; separated from paravomerine teeth by two and one-half times diameter of a choana; a distinct sublingual fold; paravomerine teeth (in a paratype) in a single patch, notched behind and partly separated posteriorly. All teeth rather brownish in color.

Costal folds, 19; 20 costal grooves, the latter distinct on dorsum, sides, and venter; body skin very smooth, not wrinkled; pits scarcely discernible under a lens; fold formed by the epibranchial cartilage can be traced the width of two costal folds behind level of arm insertion; a white postiliac glandular area; 19th costal groove does not reach below upper level of leg insertion; vent short (1.8 mm.); walls strongly papillate (a small spermatophore present in cloaca).

Arm and leg small, their length equal to 2.5 costal folds, separated by 14 costal folds; four fingers, inner rudimentary; third largest and longest, rather pointed, the tip free; five toes, the second toe rounded; others involved in skin of sole; second and third fingers with little or no web, fused to each other.

Color: Above and on sides dark grayish slate with a narrow median area showing some brownish coloration; ventral coloration gray-brown to grayish, definitely lighter than sides; a cream line hidden by a gular fold; dim cream markings on dorsal surface of thigh and upper arm; a white mark covering postiliac gland; tail colored like body; upper lip with a median light area; limbs lighter than body.

Measurements: (See table).

Remarks: Five specimens were taken, of which four were in rotting logs containing the old burrows of insect larvae. In the same logs were found *Oedipina cyclocauda.* One specimen was found

by R. C. Taylor under a small rock at the edge of a flowing stream.

No. 29968 (tip of tail lost) is brownish, the slaty-gray color not being in evidence. It has, perhaps, recently shed.

MEASUREMENTS AND DATA ON TYPE AND PARATYPES OF OEDIPINA GRACILIS

MUSEUM	KUMNH	KUMNH	RCT	RCT	KUMNH
Number	29970	29968	1420	1419	29969
Sex	♂	♀	♂	♀	♂
Snout to vent (body length)	41.3	41	41	37	41
Snout to foreleg	9.5	9.1	9	8.3	10
Axilla to groin	27.5	27.2	27.7	24	27.6
Length to gular fold (head length)	6.3	6	6.4	6	6.2
Snout to lateral nuchal groove	7	7.1	7.4	6.6	7.3
Width of head	3.9	4	3.7	3.5	4
Tail length	78 +	57	105.?	65	107
Arm	3.1	4.5	3.9	3	3.4
Leg	3	5	4.1	3.6	3.6
Head width in body length	10.6	8.2	11	10.3	10
Head length in body length	6.45	6.83	6.4	6.16	6.8
Costal grooves	20	19	20	20	20
Costal folds	19	18	19	19	19
Caudal folds	61 +	48 +?	83?	57	86
Maxillary teeth	23-22	16-18	21-21	17-18	19-18
Mandibular teeth	25-25	38-37	31-31	26-26	27-26
Premaxillary teeth	1	3	2	3	2
Vomerine teeth	9-10	7-7	9-9	7-8	7-7
Paravomerine teeth (approx.)	120	120	144	145	?

Oedipina pacificensis sp. nov.

Plate LXXXVII, fig. 2; text fig. 12

Type: Kansas University Museum of Natural History No. 29965 ♀; collected August 23, 1947, about two miles east of San Isidro El General, C. R., at an elevation of approximately 2118 feet, by Edward H. Taylor.

Diagnosis: A species 42.5 mm. snout to vent; tail 77 mm. (regenerated tip); eye length a little less than snout length; costal grooves 19, visible on venter; caudal vertebra 50 +; tail rounded for greater part of length, toward tip somewhat compressed; an indefinite depression at base of occiput; maxillary teeth present but reduced in number 12-14; vomerine teeth 8-8; premaxillary teeth 4; paravomerine series with approximately 112 teeth, all on same level; head brown, and a broad brownish stripe from head to base of tail; neck and side gray-slate; limbs light brown, separated when adpressed by 13.5 costal folds; a pair of light spots behind eyelids.

Description of the type: Species of small size for the genus; width of head contained in snout-to-vent length 12.6 times; head length in same distance, 7.4 times; head flat, low, the depth just back of eye 2 mm.; snout narrowed, but not "pointed," there being a very slight medial emargination at tip; nostrils minute, the groove run-

ning from nostril directed backward and downward to the very small subnarial swelling; a distinct groove outlines the inner border of eyelid and continues back from eye to the nuchal groove; back of eye a short distance, a groove arising on side of head crosses the chin and jaw, touches but does not bisect the postorbital groove; the chin groove forms a curve on the mesial half of the chin and two narrow slightly converging grooves run forward from it and terminate near the anterior part of chin; gular fold crosses throat, curving strongly forward; on sides groove continues to near median dorsal line; posterior part of epibranchial cartilage continues above arm to second costal groove (counting an axillary groove); head (3.6 mm.) a little wider than body (3.3 mm.); no groove from nostril directed backward, the loreal area somewhat inflated; snout rounded in lateral profile; top of head strongly pitted and corrugated; glands on head and to a somewhat lesser extent on body, forming minute circular cream spots visible under a lens; eye large, the length 1.8 mm. (free edge of upper lid), 1.25 times axial length of snout (from a line across front of eyes to median tip); width of eyelid in interorbital distance, 1.5 times.

Tongue free (rather far back in mouth), only a rudiment of a sublingual fold present; maxillary teeth present, 12-14, reaching back on side somewhat behind outer end of vomerine series; two, possibly three, premaxillary teeth, separated narrowly from maxillary teeth; vomerine teeth 8-8 in a strongly elevated series arising behind and about level of middle of choanae, running in and curving back somewhat; choanae large, somewhat transversely oval; the diameter of one in distance between them, three times; palatal area in front of vomerine ridges (seen from below) much more elevated than region posterior to the ridges; paravomerine tooth series forming a single patch, slightly notched behind, separated by half length of one vomerine ridge from the vomerine series; total number of paravomerine teeth approximately 112; mandibular teeth 14-14.

Costal grooves 19-19; limbs each equal in length to two folds; when adpressed separated by 13.5 folds; limbs short, the hand about .7 mm. in width bearing four digits; inner digit reduced, the tip not free; third longer than second, free only at tip; fourth much shorter than either second or third, its tip barely free; foot .8 mm. in width with five toes, the third toe longest, the tips of the three median free and rounded; first and fifth short but distinct, the tips not free.

A small postiliac gland present; skin of body smooth or shallowly pitted; lateral costal folds with longitudinal wrinkles; tail subcircular, now somewhat shrunken; 50 caudal grooves; the terminal part of tail somewhat compressed, with a short, recently regenerated part; no obvious constriction at base of tail.

Color: Head brown with an irregular whitish area back of each eye on dorsal part of head (scarcely discernible in preserved specimen); eyelids blackish; edge of both upper and lower eyelid dimly bordered with dirty white; a whitish, roughly-triangular spot at tip of snout on upper lip; remainder of top and sides of head brownish; a median stripe of brown from head to base of tail; sides and

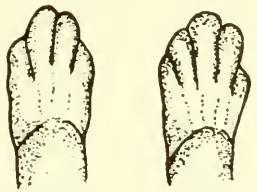

FIG. 12. *Oedipina pacificensis.* Type. A. Left hand, dorsal view. B. Left foot, dorsal view. (Much enlarged.)

tail slate; arms and legs light brown with a white spot on under side at joint, and a whitish spot below insertion of limbs; chin dirty whitish; venter and underside of body grayish slate; a postfemoral white spot covering gland; nuchal groove on throat white.

Measurements in mm.: Snout to end of vent 43; length of tail 77+; snout to fore leg 10; axilla to groin 29; snout to nuchal groove (medial ventral) 6; snout to (lateral) nuchal groove 7; head width, 3.6; eye to nuchal groove (lateral) 5; arm 3.8; leg 4.

Oedipina inusitata sp. nov.

Plate LXXXVII, fig. 3; text fig. 13

Type: Kansas University Museum of Natural History No. 29964 ♀; collected three miles northeast of Santa Cruz, on the southern face of Volcán Turrialba, Costa Rica, at an elevation of approximately 6500 ft., Aug. 9, 1947, by Edward H. Taylor.

Diagnosis: A species, 44.2 mm. from snout to vent, the tail double this length (88.8 mm.); eye as long or longer than snout; snout

blunt; costal grooves 19, not visible on ventral surface; approximately 70 caudal vertebrae, tail flattened below at base, and compressed somewhat toward tip; a deep elongate nuchal pit at base of occiput (presumably normal); skull not strongly ossified (probably largely cartilage); 19-19 maxillary teeth; vomerine teeth 9-4 + on strongly elevated ridges more or less continuous across jaw; paravomerine teeth in two groups, in contact anteriorly, then diverging somewhat; from near the middle of series posterior part strongly deflected downward; combined width 1½ times in total length of the series; general color gray-black above; grayish below.

Description of type: Species of moderate size; width of head (4.1 mm.) contained in snout-to-vent length (44.2 mm.) about 10.7 times; head length (6 mm.) to nuchal groove (medial ventral) in

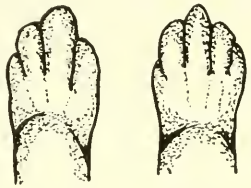

FIG. 13. *Oedipina insitata.* Type. A. Right hand, dorsal view. B. Right foot, dorsal view. (Much enlarged.)

same distance 7.3 times; (lateral measurement of head to nuchal groove 7 mm.). Head very slightly wider than body; dorsal portion of head somewhat depressed (due presumably to the poorly ossified condition of the skull); snout blunt, rounded; no groove or depressed area following nostril; snout rounded in lateral profile; top of head strongly pitted, the pits distinct, the skin minutely corrugated; no groove bordering inner edge of eyelids; width of eyelid at least twice in interorbital distance; a groove from eye running back to nuchal groove, bisecting a vertical groove on side of head; latter groove runs across jaw and chin forming an irregular line curving back somewhat mesially; a pair of narrow symmetrical grooves run forward from this line terminating near tip of chin; nuchal fold crosses neck, curving forward medianly, the fold ample; on sides of neck the groove can be traced to median dorsal line; a deep pit, a half millimeter long, at base of occiput with a groove entering from both sides; posterior extension of epibranchial carti-

lage reaches a little behind arm insertion; costal grooves 19, the grooves rather dim, there being little or no trace of the grooves across the venter; over much of body surface skin with fine longitudinal wrinkles; a strongly-defined white glandular spot behind insertion of hind limb; tail slender, not or scarcely constricted at base; under surface with a narrow flattened surface, tail becoming laterally compressed toward tip; tail twice length of head and body. Limbs small, when adpressed, separated by 13½ costal folds; hand with four digits, the third longest, bluntly pointed; second longer than fourth; foot with five digits, the first greatly reduced and scarcely discernible; first, second and third equally broad, the latter longest; the second and fourth equal; fifth toe narrow, a little longer than first; digits free only at extreme tip. Maxillary teeth 19-18; premaxillary teeth 5 in an uneven row; vomerine teeth 9-10; mandibular teeth 23-23; vomerine teeth curving from outer edge of choanae; paravomerine teeth in two slightly separated series touching anteriorly, slightly separated posteriorly, not on same level but just anterior to middle of series strongly deflected; choanae large, the diameter of one contained in distance between the two a little more than three times.

Measurements in mm.: Snout to vent 44.2; length of tail 88.8; snout to foreleg 9; axilla to groin 29.5; width of head 4.1; length of head to nuchal fold (median ventral point) 7.3; length of arm 3.2; length of leg 4.

Color: Above and on sides of body grayish black, the ventral surface of body and tail grayish; top of head brownish, except that eyelids are blackish above with a light area on outer edge; edge of upper lip light brown or cream; chin light cream with some pigmentation forming some small indistinct rounded lighter spots; nuchal groove and fold and an area below arm insertions, cream. On top of head the skin glands are outlined by a dark reticulation.

Remarks: This species, in the unusual character of the paravomerine teeth, the compressed tail, the dorsal nuchal pit, the poorly ossified skull, seems to be separated amply from the other species of the genus.

The type specimen was taken from under a rotting log under which was also found a specimen of a black-and-red leech rolled into a ball and occupying a rounded depression. When placed in the collecting bag the leech seized the salamander almost immediately, causing the salamander to struggle to escape. It was necessary for me to bring about the separation. The type locality

is in cut-over forest near some open fields on the southern slope of Volcán Turrialba at an elevation of approximately 6500 feet.

Oedipina alfaroi Dunn

Oedipina alfaroi Dunn, Proc. Biol. Soc. Washington, vol. 34, 1921, p. 145 (type locality, Zent, Costa Rica, E. R. Dunn coll.); Taylor, Univ. Kansas Sci. Bull., vol. 30, pt. 1, May 15, 1944, pp. 226-227.

Oedipus alfaroi Dunn, Field Mus. Zool. Ser. vol. 12, 1924, p. 99; The Salamanders of the Family Plethodontidae. Smith College Publ., 1926, pp. 435-436, fig. 86.

Diagnosis: An elongate form with 20 costal grooves; eye proportionally small, distinctly shorter than the snout; teeth absent on maxilla; one premaxillary tooth; limbs short, separated by a distance equal to length of 14 costal folds.

Description: (Museum Comp. Zool. Harvard No. 6938, type.) Elongate body, the head not or scarcely equal to width of body; eye proportionally small, its length (1.2 mm.) distinctly less than snout length (2 mm.); snout oval rather bluntly pointed; posterior ends of eyelids fitting under a diagonal fold; groove from eye to lateral gular fold very indistinct or absent anteriorly; a groove crossing jaw and passing under chin to opposite side; a pair of lines running forward from this on chin to form an incomplete arch; the gular fold curves forward on neck, the groove lacking pigment; head width approximately 12 times in snout-to-vent length; head length 7 times in same distance. Twenty grooves on body; 19 costal folds; at least 63 caudal folds on complete tail; arm and leg slender, the digits united with only tips of two inner fingers and three inner toes free; when limbs are adpressed they are separated by 14 costal folds; tail not or very indistinctly constricted at base, circular in cross section; vomerine teeth in two series of about 9 teeth each, beginning at outer level of choanae and curving back; the series separated from each other by a distance equal to diameter of choana; paravomerine teeth in a single patch; no maxillary teeth; one premaxillary tooth not penetrating the lip; mandibular tooth series present on front half of jaw; a small glandular spot behind insertion of hind limb. Skin very smooth above, the pits not distinct; a small sublingual fold.

Color: Above rather lavender to purplish brown, light grayish below; postiliac glandular spot whitish.

Measurements in mm.: Snout to end of vent, 61; head width, 5.1; head length to gular fold, 7.5; tail (regenerated), 43.5; arm, 4; leg, 4.6.

Remarks: I have examined the type and paratype from Zent and a specimen from Suretka. The latter specimen has a tail length of 104 mm., and a snout-to-vent length of 54.5 mm., slightly more than half of the tail length.

The relationship of this species is with *Oedipina elongatus* Schmidt from Guatemala and Chiapas.

CAECILIANS

ORDER GYMNOPHIONA Müller

Gymnophiona Müller, Zeitschr. Physiol., vol. 4, 1832, p. 24.

FAMILY CAECILIIDAE Gray

Caeciliidae Gray, Ann. Philos., ser. 2, vol. 10, 1825, p. 217.

Two genera, *Dermophis* and *Gymnopis*, are recognized in Costa Rica.

KEY TO GENERA OF COSTA RICAN CAECILIIDAE

1. An eye present; without an inner row of mandibular teeth, *Dermophis*
   No eye; an inner mandibular tooth row ..... *Gymnopis*

Animals belonging to the Gymnophiona bear a striking resemblance to earthworms. They lack limbs and in color are usually dark lead, slate or occasionally lavender. They are commonly called caecilians.

Genus DERMOPHIS Peters

Dermophis Peters, Monatsb. Akad. Wiss. Berlin, 1879, pp. 930, 937.

Type of genus: *Siphonops mexicanus* Duméril, Bibron and Duméril.

Only a single form of this genus is known to occur in Costa Rica.

Dermophis mexicanus gracilior Günther

Plate LXXXVIII

Dermophis gracilior Günther, Biologia Centrali-Americana: Reptilia and Batrachia, Jan. 1902, p. 306, pl. 76, fig. B (Chiriquí, Panamá); Nieden, Das Tierreich, Gymnophiona, 1913, p. 9.

Dermophis mexicanus gracilior Dunn, Proc. New England Zool. Club, vol. 10, p. 73; Bull. Mus. Comp. Zool. Harvard Coll., vol. 91, Dec. 1942, pp. 447-478 (Pozo Azul, Costa Rica. Also Panamá records).

The following described specimen from San Isidro El General has been referred to this form with some hesitation, since it differs in several points from the published data on *gracilior*. Since the specimen is young, the discernible color characters, and those of the skin glands may be those of youth. The reduced number of primaries and secondaries is approached by a specimen listed

by Dunn (1944). Sufficient Costa Rican specimens may warrant the placing of these in another subspecies.

Diagnosis: Eyes distinct, tentacle closer to eye than nostril; 93 primaries (not counting nuchal grooves), the first 47 lacking secondaries; 49 secondaries; no inner mandibular teeth present; a deep short secondary groove on first nuchal fold, and another shallow

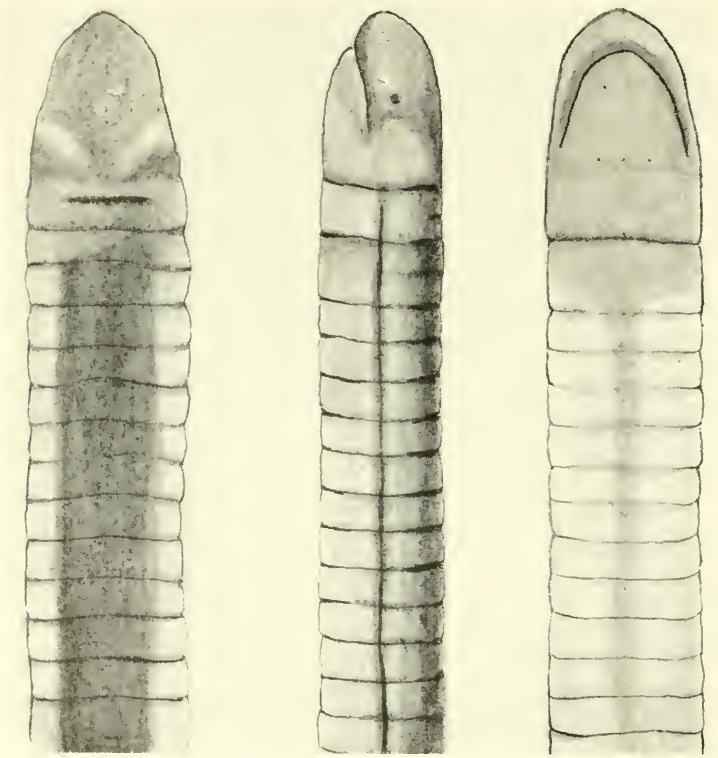

PLATE LXXXVIII. *Dermophis mexicanus gracilior* Günther. K.U.M.N.H. No. 29979. San Isidro El General, Costa Rica. Width of head, 6 mm.

groove on the second fold; total length, 160.5 mm.; a broad dorsal stripe of purplish lavender, darker dorsolaterally on outer edges; this bordered anteriorly by a narrow light lavender stripe; below clouded with lavender on a cream ground-color.

Description of subspecies: (K.U.M.N.H. No. 29979). Body moderately thick, the general width of body (8 mm.) in total length (161.5 mm.) about 20 times; snout subconical; eye visible, its lower edge about 1.15 mm. above edge of lip and 3.5 mm. from tip of

snout; tentacle surrounded by a circular groove closer to eye than to nostril; maxillary-premaxillary tooth row continuous, with total of 30 teeth, curving slightly back, those in the premaxillary part of series a little larger than others; prevomerine-palatine series of approximately 40 very small teeth; outer mandibular row of 26 teeth, very unequal in size, teeth diminishing toward posterior part of the series, the teeth larger than those in maxillary series; no inner mandibular teeth; choanae moderate, their anterior edges about 1 mm. behind the front end of prevomerine tooth series. Inner part of mouth in area between the upper tooth rows and in region anterior to choanae, with small dark punctations; also some punctations around the choanae and on the sides of the palate (probably small glands). First two annular folds differ from those on body; first groove curving a little on dorsal surface is slightly farther forward on venter than above; the second groove corresponding to the nuchal and gular fold (or groove) of salamanders is deeper than the preceding; third annular groove moderately distinct. Width of the two nuchal folds is 2.7 mm. and 3.2 mm. respectively; there are two secondary grooves on these folds, the first short and deep on middorsal surface, the second not deep but distinct on dorsum and sides; on each side in front of first groove two small moundlike elevations, separated mesially. The first 47 body primaries lack secondaries; total primaries 93; total secondaries 46 (22 of which encircle the body); vent with edges swollen and 6 denticulations on each border.

Color: The dorsal coloration consists of a broad purplish lavender stripe darker on dorsolateral edges, sharply delimited; each side of this bordered by a narrow discrete light lavender stripe anteriorly, below which the color is dirty cream, clouded with some sparse lavender pigment. This is continued on to venter, which is dull cream near the middle, almost without pigment; anal region and area about the tentacle, cream white; chin and throat grayish anteriorly; beginning near neck and continuing an indefinite distance; there is a median narrow ventral dark line.

Measurements in mm.: Snout to vent 159; vent to end of body 1.5; width of head at first groove 6; widest part of neck 6.6; distance between tentacle and nostril 1.9; between tentacle and corner of mouth 3.9; tentacle from eye 1.5; distance from eye to nostril 4; nostril from snout tip 1; nostril from edge of lip 1.9; 1st groove from tip of chin 5.2; 1st groove to end of snout 7; from end of second fold to tip of snout (ventral) 13.

Remarks: A distinctive character of this form is the presence of the greatly enlarged skin glands following the lines of the primaries and likewise of the secondaries. These are evident externally to the naked eye as small subcircular depressions almost contiguous, and by the yellow or cream color of the glands. In size these are five or six times larger than the other skin glands. They are visible under a lens as small cream or white punctations in a fine reticulum of lavender. On the ventral surface the glands are visible but the lavender reticulum may be entirely wanting, or a very sparse amount may be present in patches. Whether or not the character of the glands is comparable to those, in *Dermophis mexicanus clarki, Dermophis parviceps* and in the adults of *gracilior,* I do not know since these forms have been inadequately described.

Genus GYMNOPIS Peters

Gymnopis Peters, Monatsb. Akad. Wiss. Berlin, 1874, p. 616.

Type of genus: *Gymnopis multiplicata* Peters.

Two forms, here treated as subspecies, are known to occur in Costa Rica.

KEY TO COSTA RICAN GYMNOPIS

Primaries 112-126; secondaries 84-104 ..... *multiplicata proxima*
Primaries 128-132; secondaries 101-111 ..... *multiplicata multiplicata*

Gymnopis multiplicata multiplicata Peters

Gymnopis multiplicata Peters, Monatsb, Akad. Wiss. Berlin, 1874, p. 616, pl. 1, fig. 1 (type locality, Veragua, collected by von Warszewicz); *idem,* 1879, p. 939, fig. 7; Boulenger (*part.*), Catalogue of the Batrachia Gradientia s. Caudata and Batrachia Apoda in the collection of the British Museum, 2nd ed., 1882, p. 100; Proc. Zool. Soc. London, 1895, p. 410; Cope, Proc. Amer. Philos. Soc., vol. 22, p. 171; Günther, Biologia Centrali-Americana; Reptilia and Batrachia, Jan. 1902, p. 308; Nieden, Das Tierreich, Gymnophiona, 1913, p. 21; Dunn, (*part.*), Proc. New England Zool. Club, vol. 10, 1928, p. 75.
Siphonops simus Cope, Proc. Amer. Philos, Soc., vol. 17, 1877, p. 91 (type locality, Costa Rica).
Gymnopis sima Cope, Proc. Amer. Philos. Soc., vol. 22, 1885, p. 171; U. S. Nat. Mus. Bull., No. 32, 1887, p. 9.

Diagnosis: Large species, the greatest known total length 510 mm.; body width in total length 25 to 35 times; eye invisible; maxillary-premaxillary tooth series approximately 40; palatine-prevomerine tooth series approximately 42; outer mandibular series approximately 32 teeth; inner mandibular tooth series, 2. Primary costal grooves on body 132 (not counting grooves on neck), 18 lacking secondary grooves; 114 secondaries, of which only about 15 surround the body completely. Color plumbeous above, the grooves distinctly lighter; venter lighter, gray-lavender.

Description of subspecies: (R.C.T. No. 970). Body elongate, the total length 390 mm.; width of body in total length 32 times; snout oval; eye invisible; tentacle surrounded by a circular groove, the surrounding swollen area three times diameter of opening, situated 4.4 mm. from nostril, 4 mm. from corner of mouth; nostril 1 mm. from tip of snout; maxillary-premaxillary teeth in a nearly continuous series of about 40, the most posterior smallest; palatine-prevomerine series with approximately 42 teeth; area between these tooth series as well as the region anterior to choanae and on sides of palate back of choanae, showing fine darker punctations which probably are glands; outer mandibular tooth row with 32 teeth, larger than the maxillary teeth on the whole, but posterior ones of the series about the size of the posterior teeth above; 2 curving teeth in inner mandibular series.

First annular groove curves farther forward above and below than on sides; slight elevations (glandular) on each side in front of first groove, not meeting mesially; second groove, transverse straight; third groove marking limit of second fold curves back on throat and is incomplete ventrally; ventral width of first and second folds 4.8 mm. and 6 mm. respectively; primary body grooves 132, 18 without secondaries; 114 secondaries, the terminal 15 completely surround body; vent transverse with two lobules on front border, eight on lateral and posterior borders.

Color: Above dark plumbeous slate, the grooves light gray, at least on anterior part of body; ventral parts dark tending to lavender near middle of body; a cream spot at vent and another behind and including the tentacle.

Measurements in mm. of Nos. 970, 29978: Snout to vent 382, 164; vent to end of body 3, 1.5; width of head at first groove 10.5, 6.4; greatest width of neck 12, 6.8; tentacle from nostril 4.5, 2.6; tentacle from corner of mouth 4, 2.5; tentacle from tip of snout 5.5, 3.2; nostril from tip of snout 1.8, .8; tip of snout to first annular groove 11, 6.1; tip of snout to second annular groove 15, 10; tip of snout to end of second fold (first body groove) 21.

Variation: The specimen differs from the type in being plumbeous-slate rather than black in coloration. A second specimen (K.U.M.N.H. No. 971), taken in the same immediate vicinity, differs but little save in size. It measures 164 mm., its width (6 mm.) in length, 27.3 times. The primaries and secondaries are very similar in number, there being respectively 133 primary body grooves and 113 secondaries. Average counts of specimens listed by Dunn (1942) for Costa Rica show the following range and

averages for primaries and secondaries respectively: 128-132, average 129; 101-110, average 106. It will be noted that the specimens have a somewhat higher average of both primaries and secondaries, but of a magnitude scarcely significant.

Variation in dentition is more significant and one concludes that teeth are added as the animal grows older and larger. The smaller specimen (K.U.M.N.H. No. 29978) has fewer teeth in the maxillary-premaxillary series (21) but if one counts the diastemata there are spaces for 31 teeth. One presumes that the later additions are made on the posterior part of the series. The palatine-prevomerine series has approximately 32 teeth, the outer mandibular series 24, and the inner mandibular series 2. In color the young is similar to the adult, with the gray lines marking the anterior grooves.

The species has been reported from the following Costa Rican localities: Tilaran, San Mateo, and Taboga. The two specimens here listed are from three miles north of San Isidro El General. They were taken from under rocks in a wet meadow.

Gymnopis multiplicata proxima (Cope)

Text fig. 14

Siphonops mexicanus Cope, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 8, 1875, p. 96 (eastern Costa Rica).

Siphonops proximus Cope, Proc. Amer. Philos. Soc., vol. 17, 1877, p. 90 (type locality, eastern Costa Rica; Wm. Gabb coll.).

Dermophis ? proximus Peters, Monatsb, Akad. Wiss. Berlin, 1879, p. 938; Boulenger, Catalogue of the Batrachia Gradientia s. Caudata and Batrachia Apoda in the Collection of the British Museum, 2nd ed., 1882, p. 99.

Gymnopis proxima Cope, Amer. Philos. Soc., vol. 22, 1885, p. 171; U. S. Nat. Mus. Bull. No. 32, 1887, p. 9; Boulenger, Proc. Zool. Soc. London, 1895, p. 410; Günther, Biologia Centrali-Americana; Reptilia and Batrachia, Jan. 1902, p. 308; Nieden, Das Tierreich, Gymnophiona, 1913, p. 21; Noble, Bull. Amer. Mus. Nat. Hist., vol. 38, 1918, p. 346.

Gymnopis multiplicata (*part.*), Dunn, Proc. New England Zool. Club., vol. 10, 1928, p. 75; Bull. Mus. Comp. Zool. Harvard College, vol. 91, 1942, pp. 466-468.

Diagnosis: A large form, reaching a known maximum length of 480 mm.; eye invisible; tentacle in a circular groove, widely separated from nostril; maxillary-premaxillary tooth series (total) 50; approximately 40 mandibular teeth, larger than the upper series; approximately 60 teeth in the prevomerine-palatine series; 6 teeth in the inner mandibular series; primaries 112 to 126; secondaries 84 to 104. Gray lavender above and on sides; dirty yellowish white below; area about vent cream; tentacle and region posterior to eye dull cream.

Description of subspecies: (K.U.M.N.H. No. 29977 ♀, Turrialba, adult female). Large, the snout to vent length 405 mm.; body width (18 mm.) in length 22.5 times; eye invisible; tentacle surrounded by a circular groove, situated nearly midway between angle of mouth and nostril; nostril 2 mm. from tip of snout; maxillary-premaxillary teeth in a continuous row containing a total of 50 teeth; teeth of the palatine-prevomerine series continuous, the teeth very small (save for a single, large anomalous tooth on one side) the number of teeth being approximately 60; outer mandibular teeth total approximately 40, varying in size, the smaller

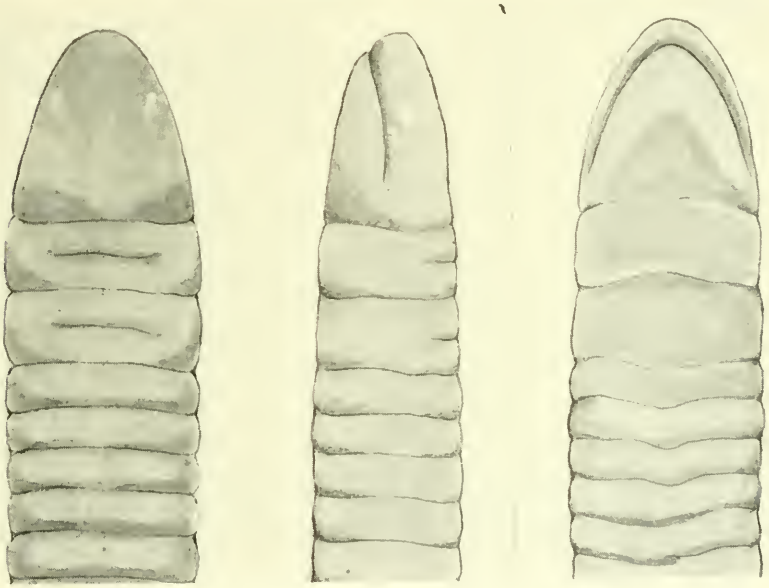

FIG. 14. *Gymnopis multiplicata proxima* (Cope) K.U.M.N.H. No. 29977, Turrialba, Costa Rica. Width of head, 14 mm.

teeth much larger than those in the maxillary-premaxillary series; 6 teeth in the inner mandibular series the teeth contiguous on each side with a slight median diastema. Choanal openings rather elongate, 3 mm. from anterior prevomerine teeth; some pigment discernible between the upper rows of teeth.

First annular fold on back of head complete curving forward dorsally and a little farther forward on chin; second groove transverse, the groove limiting the second fold not complete on ventral surface; width (ventral) of first two folds, 5 mm. and 7.5 mm. re-

spectively; there are secondary grooves on both folds confined to dorsal surface; primary body grooves 22 + 98; secondary grooves 98; only the last ten completely surround body; preceding first neck fold are two very slight elevations dorsolaterally, not meeting mesially.

Skin glands in adult not visible through the skin; vent with 8 posterior denticulations on sides and posterior edge; two large lobules on anterior edge.

Color: In life there was a grayish ultramarine cast on dorsal and lateral surfaces, the venter dull dirty cream; tentacle and an area behind it, cream; an area about vent cream.

Measurements in mm.: Snout to vent 402.2; vent to end of body 2.8; width of head at first groove 14; greatest width of neck 14.8; width of body 18; tentacle to end of snout 7; nostril to end of snout 2; first groove to tip of snout (ventral) 12.6; to second groove 18; to first annular body groove 25.

Variation: Two small specimens (R. C. T. Nos. 331-332) are at hand. The first was found with the larger No. 29977, the second was taken from the uterus. They measure 131 and 128 mm. in length respectively. The top of the head is darker, the color coming to a point behind on middorsal line at the first groove. The body is lavender-slate, distinctly lighter below. In these, the skin glands are visible under a lens. On the first two folds certain larger glands are thickly scattered. At succeeding grooves there is a regular transverse line of larger grooves visible under the lens. These can be traced around the body with occasional interruptions; they occur also in the secondary grooves. The characteristic grooves forming the lobules or denticulations about the vent are evident in the two young.

Dunn (1942) lists numerous specimens from various localities in Panamá, Costa Rica, and Nicaragua. The variation in the primaries and secondaries for the three countries is as follows:

Panamá 115-125; 85-101; average 118.5, 94.

Costa Rica, 112-124; 84-104; average 119, 93.5.

Nicaragua, 118-126; 95-103; average 121, 98.

Costa Rican localities for this subspecies are: Suretka, Limón, Monteverde, Reventazón, Guápiles, Cariblanco, Peralta, Parismina and 5 km. north of Cartago. Specimens reported in this paper are from Turrialba. They were found in a pile of rocks.

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Describes *Magnadigita nigrescens*, *Bolitoglossa palustris*, *Parvimolge richardi* and *Oedipina serpens*.

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Twelve salamanders with three species reported.

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Third Contribution to the Herpetology of San Luis Potosí

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ABSTRACT: An annotated report is made on an herpetological collection belonging to the Louisiana State University, consisting of 525 specimens from various localities in the Mexican State of San Luis Potosí. The specimens represent 65 species and subspecies (or varieties) of the following groups: 20 amphibians, 3 turtles, 20 lizards, and 20 snakes. Thirteen species and subspecies are reported from the State for the first time.

This paper represents a continuation of my studies on the herpetological fauna of the Mexican State of San Luis Potosí. The material on which it is based is a recent collection made by Dr. George H. Lowery, Mr. Robert Newman, Mrs. Marcella Newman, Mr. Walter Dalquest, Mr. A. N. Robinson, and Mr. S. A. Arny, all members of a party from Louisiana State University primarily engaged in ornithological research. For the privilege of examining this collection, as well as the two others previously studied, I am indebted to Dr. George H. Lowery, Director of the Museum of Natural History at Louisiana State University.

My previously published papers° report a total of 144 species and subspecies, distributed as follows: salamanders 5, Salientia 25, turtles 3, lizards 33, snakes 78.

Seven additional species are listed in Smith and Taylor U. S. Nat. Mus. Bull., 199, 1950, p. 226. These include one turtle and six lizards as follows:

Kinosternon hirtipes †
Holbrookia maculata dickersonae
Lepidophyma smithi occulor
Gerrhonotus liocephalus infernalis ‡
Cnemidophorus sackii communis
Anelytropsis papillosus
Leiolopisma caudaequina

° A preliminary account of the herpetology of the State of San Luis Potosi, Mexico, Univ. Kansas Sci. Bull., vol. 33, pt. 1, 1949, pp. 169-215. Second contribution to the herpetology of San Luis Potosí, Univ. of Kansas Sci. Bull., vol. 33, pt. 2, 1950, pp. 441-457, pls. 4-9.

† Possibly a doubtful record.

‡ Possibly based on the form recently designated as *Gerrhonotus liocephalus loweryi*.

One frog, *Rana moorei* § recently described is included. Ten species added in the present study are:

SALAMANDER

Ambystoma velasci Dugès

SALIENTIA

Rhinophrynus dorsalis Duméril and Bibron
Bufo occidentalis Camerano
Rana montezumae Baird
Rana catesbeiana Shaw

TURTLES

Kinosternon cruentatum cruentatum Duméril and Bibron

LIZARDS

Cnemidophorus sackii scalaris Cope

SNAKES

Ninia diademata plorator Smith
Lampropeltis getulus splendida (Baird and Girard)
Pituophis sayi affinis Hallowell

This brings the total number of forms listed approximately to 162, distributed as follows: salamanders, 6; Salientia, 30; turtles, 5; snakes, 81; lizards, 40.

Only the Mexican states of Oaxaca and Veracruz are known to have a larger snake fauna (99 each); at least six states, Baja California (high with 87 forms), Chiapas, Guerrero, Oaxaca, Sonora, and Veracruz have larger lizard faunas; while the number of amphibians is greater in the following states: Chiapas, Guerrero, Oaxaca, Puebla and Veracruz (high with 71 forms).

Owing to certain revisionary work of other herpetologists and the discovery of errors in the literature, some changes are necessary in the names of certain species listed in my previously published papers on the fauna of San Luis Potosí. A list of these changes follows:

Scaphiopus multiplicatus Cope = *Spea multiplicata* (Cope)
Bufo simus (*nec.* Schmidt) = *Bufo occidentalis* Camerano
Anolis sericeus (*nec.* Hallowell) = *Anolis sallaei* Günther

§ *Rana moorei* A. P. Blair from Arroyo Sacahuite at Palictla, 6 miles by highway north of Tamuzunchale, S. L. P. Amer. Mus. Novitates no. 1353, 1947, pp. 1-17.

Sceloporus microlepidotus disparilis = *Sceloporus grammicus disparilis* Stejneger

Sceloporus ferrariperezi melanogaster = *Sceloporus torquatus melanogaster* Cope

Cnemidophorus gularis gularis = *Cnemidophorus sackii gularis* Baird and Girard

Thamnophis sauritus proximus = *Thamnophis sirtalis proximus* (Say)

Thamnophis macrostemma megalops = *Thamnophis eques megalops* (Kennicott)

Elaphe laeta laeta = *Elaphe emoryi emoryi* (Baird and Girard)

A list of the forms treated in this paper is given herewith:

AMPHIBIA

Ambystoma velasci Dugès
Scaphiopus couchii Baird
Scaphiopus sp.?
Spea multiplicata (Cope)
Rhinophrynus dorsalis Duméril and Bibron
Bufo valliceps Wiegmann
Bufo valliceps var.
Bufo horribilis Wiegmann
Bufo coguatus Say
Bufo punctatus Baird and Girard
Bufo occidentalis Camerano
Syrrhophus latodactylus Taylor
Hyla eximia Baird
Hyla arenicolor Cope
Hyla miotympanum Cope
Smilisca baudinii (Duméril and Bibron)
Hypopachus cuneus cuneus Cope
Rana montezumae Baird
Rana pipiens Schreber
Rana catesbeiana Shaw

TURTLES

Terrapene mexicana mexicana (Gray)
Kinosternon integrum Leconte
Kinosternon cruentatum cruentatum Duméril and Bibron

LIZARDS

Anolis sallaei Günther
Ctenosaurus acanthura (Shaw)
Crotaphytus collaris baileyi Stejneger
Phrynosoma orbiculare orbiculare (Linnaeus)
Phrynosoma modestum Girard
Phrynosoma cornutum (Harlan)
Holbrookia maculata approximans Baird
Holbrookia texana (Troschel)
Sceloporus parvus parvus Smith
Sceloporus variabilis variabilis Wiegmann
Sceloporus grammicus disparilis Stejneger
Sceloporus spinosus spinosus Wiegmann
Sceloporus torquatus melanogaster Cope
Sceloporus serrifer plioporus Smith
Sceloporus jarrovii minor Cope
Lepidophyma smithi occulor Smith
Cnemidophorus sackii scalaris Cope
Cnemidophorus sackii gularis Baird and Girard
Cnemidophorus sackii communis Cope
Barisia imbricata ciliaris (Smith)
Eumeces tetragrammus (Baird)
Eumeces lynxe lynxe (Wiegmann)

SNAKES

Heterodon nasicus kennerlyi Kennicott
Ninia diademata plorator Smith
Dryadophis melanolomus veraecrucis Stuart
Elaphe emoryi emoryi (Baird and Girard)
Lampropeltis getulus splendida (Baird and Girard)
Masticophis flagellum lineatulus Smith
Masticophis flagellum testaceus (Say)
Drymarchon corais erebennus (Cope)
Pituophis deppei jani Cope
Pituophis sayi affinis Hallowell
Thalerophis mexicanus mexicanus (Duméril, Bibron and Duméril)
Tropidodipsas sartorii sartorii Cope
Natrix rhombifera blanchardi Clay
Thamnophis eques eques (Reuss) Smith
Thamnophis sirtalis proximus (Say)
Storeria dekayi texana Trapido
Storeria storerioides (Cope)
Bothrops atrox asper (Garman)
Crotalus lepidus lepidus (Kennicott)
Crotalus atrox Baird and Girard

I wish to acknowledge assistance from the following persons: to Dr. Hobart M. Smith, who examined certain puzzling specimens

FIG. 1. Map of San Luis Potosí, showing collecting localities.

and assisted in their identification; Mr. Leslie Burger for the identification of certain *Cnemidophorus*, and to Dr. L. M. Klauber for the data on the rattlesnakes now in his hands. Dr. George Lowery has kindly prepared the map that is included.

SALAMANDERS

Ambystoma velasci Dugès

Ambystoma velasci Dugès, La Naturaleza, ser. 2, vol. 1, 1888, p. 142 (Substitute name for *Siredon Tigrina* Velasco.) (Type locality, Laguna Santa Isabel, near Guadalupe, Hidalgo, Distrito Federal, México.)

Four larvae and one transformed specimen are in the collection. Nos. 2486-2489 are from 1 km. N Arenal; No. 2490 from 2 km. NE Arriaga. These are the first records of a form of *Ambystoma* from San Luis Potosí.

The larvae closely resembles those of this species from the Valle de México, in the region of the type locality. The transformed young specimen is dark gray with 40 or more small irregular white spots on head and body. The spots on the tail are larger and are on the dorsal part only. The ground color on the tail is darker than that on the body. On the ventral surface of the head and body, the larvae and transformed young are white.

SALIENTIA

Scaphiopus couchii Baird

Scaphiopus couchii Baird, Proc. Acad. Nat. Sci. Philadelphia, vol. 7, 1854, p. 62 (type locality, Matamoras, Tamaulipas [restricted]).

Nos. 2042, 2046-2067. A series of 22 specimens were taken at Hacienda Capulín, on June 21 and June 25; the number of males is 15, of females 7. The males of the series vary in snout-vent length from 54-62 mm. and have a maximum head width of 28 mm. and a maximum leg length (from vent) of 75 mm. The females vary between 54 mm. and 60 mm. in snout-vent length, the maximum head width being 28 mm., the maximum leg length, 70 mm.

The vomerine teeth in the specimens are usually in two fasciculi, between the choanae beginning about the middle and extending at least half their width behind the posterior level of the choanae, separated mesially by a distance greater than that separating them from the choanae. However, there is surprising variation in this character and on occasion the teeth are in two diagonal fasciculi at the end of a ridge originating at the inner anterior edges of the

choanae, the teeth almost or completely behind the hinder level of the choanae.

In all cases the skin of the dorsal part of the head is fused to the bone. The parotoids, if present, are not externally discernible. All specimens are equally tubercular, the tubercles rather small and more or less equally distributed on dorsal and lateral surfaces. Three fingers bear nuptial asperities in the males.

Scaphiopus sp.

No. 2042. Tepeyac. This specimen, in an indifferent state of preservation, differs from the preceding *couchii* in having a snout to vent measurement of 70 mm., the eyes less prominent, the leg, 76 mm. from vent; the femur more completely involved in the integument; and the webbing on the feet somewhat more incised. The skin on the head, however, is similar to that in *couchii*.

The choanae are much narrower transverse slits; the vomerine fasciculi are at the end of a ridge, arising on the inner edge of the slit and converging, separated mesially by a narrow distance. The openings of the palatal glands are two very narrow slits, widely separated, on a level midway between choanae and the front of the palate. The specimen may represent a distinct species but additional specimens must be obtained before the matter may be determined satisfactorily.

Spea multiplicata (Cope)

S[*caphiopus*] *multiplicatus* Cope, Proc. Acad. Nat. Sci. Philadelphia, vol. 15, 1863, p. 52 (type locality, Coyoacan, Distrito Federal, Mexico [restricted]).

Nos. 2043, 2045, Tepeyac, June 14, 1950; 2068-2094, Salinas, July 29-Aug. 1, 1950; 2095-2119, 2102, 2202, Hernandez, Aug. 9-11; 2508-2511, 2500-2501, 6 km. S Matahuala; 2512-2518, Presa de Guadalupe; 2519, 19 km. SW Ébano.

When the Mexican species of the genus *Spea* are revised it is possible that subspecific forms may be recognized in the varied populations of northern Mexico. Since the various listed localities are represented by gravid females it would appear that the breeding season may continue at least for two months, from June 14 to Aug. 11.

Rhinophrynus dorsalis Duméril and Bibron

Rhinophrynus dorsalis Duméril and Bibron, Erpétologie générale, vol. 8, 1841, pp. 758-760, Atlas, 1854, pl. 91, fig. 2, 2a (type locality, Veracruz, Veracruz, Mexico).

Two very young specimens, Nos. 2496, 2497 are in the collection from 19 km. SW Ébano. This is the first record for San Luis Potosí.

However they have been reported from localities farther north in Tamaulipas.

The specimens are too young for comparison with populations occurring in southern Mexico.

Bufo valliceps Wiegmann

Bufo valliceps Wiegmann, Isis von Oken, vol. 26, 1833, pp. 657-659 (type locality, Veracruz, Mexico [restricted]).

This series, for the most part, shows variation no greater than is typical of the species. The largest specimen, a female, is 95 mm. snout to vent, with a head width of 39 mm. Differing from most other specimens, the venter displays numerous black scattered flecks. The vocal slits in the males are paired in every case. Young females have the feet more slender than males of equal length. Several of the males lack the lateral markings, and the dorsal markings are reduced or obsolescent.

The localities are: Nos. 2140-2160, 7-8 miles east (by road) of Santa Barbarita, 3900 ft. elev.; 2137, 3 mi. S Ajinche; 2161-2168, Tamuzunchale; 2138, 2139, 2181, vicinity of Xilitla; 2136, vicinity of Ébano.

Bufo valliceps var.

Nos. 2174-2178, Hda. Capulín.

This series of specimens has the general superficial appearance of *Bufo valliceps* but there are certain differences that point to a distinct population.

The most significant difference is in the width of the head and the considerably shorter limbs in proportion to the length of the body.

A comparison of the major measurements (in mm.) of three males of *Bufo vallicaps* from three localities with two males from Hda. Capulín, all of nearly equal snout-to-vent length, will reveal considerable difference.

COMPARATIVE MEASUREMENTS OF BUFO VALLICEPS FROM VARIOUS LOCALITIES

	Tamuzunchale	Xilitla	Sta. Barbarita	Hda. Capulin	
Snout to vent	69	70	70	70	68
Arm length	47	46	46	38	41
Leg length	93	91	89	80	82
Head width	28	31	30	25	25
Head length	22	24	22	20	19

Most of the males agree generally in color and markings with typical *B. valliceps*. However in no. 2177, the largest female of the

series (80 mm.), the dorsal coloration is largely black and the dorsolateral light line, narrow and irregular. The male, no 2178, is dark, the lighter areas much obscured. The supraorbital crests are less elevated and the occipital crests are shorter and lower than in the other males from Capulín. Other less striking differences may also be found. *Bufo valliceps* has a wide distribution from Texas to middle or lower Central America and one may anticipate that certain variant populations may be named when the species is reviewed. The locality, Hda. Capulín, is, I believe, the western-most record of the species for San Luis Potosí.

Bufo horribilis Wiegmann

Bufo horribilis Wiegmann, Isis von Oken, vol. 26, 1833, pp. 654-655 (type locality, Veracruz, Veracruz, Mexico [restricted]).

Nos. 2120-2135, adults; 2169, 2185-2198, juvenile specimens all taken in the region about Tamuzunchale, for the most part, 1 mi. S on the Río Moctezuma. Most of the adults are males, the skin extremely rough with minute black horny spines. The parotoids are deep black or blackish brown. The digit tips and tubercles are covered by black horn. Maximum size of specimens are, ♀ 136 mm., ♂ 125 mm., the average for the adult males being 113 mm.; of the two females 131 mm.

Bufo cognatus Say

Bufo cognatus Say, *in* Long's account of an Expedition from Pittsburgh to the Rocky Mountains, vol. 2, 1823, p. 190 (type locality, Arkansas River, Prowers County, Colo.).

Nos. 2182-2184. Three specimens of this widespread species were taken at Salinas. The elongate vocal slit of the single male, no. 2182, is dextral.

Bufo punctatus Baird and Girard

Bufo punctatus Baird and Girard, Proc. Acad. Nat. Sci. Philadelphia, vol. 6, 1852, p. 173 (type locality, Río San Pedro, Val Verde Co., Texas).

No. 2044, Tepeyac; nos. 2502-2506, Presa de Guadalupe, are present in the collection. In males the vocal slits are much elongated and are present on both sides of the mouth, and the first two fingers have a considerable area of nuptial asperities, the third only a very small area on its inner edge.

Bufo occidentalis Camerano

Bufo occidentalis Camerano, Atti R. Accad. Sci. Torino, vol. 14, 1878, p. 887 (type locality, Mexico); Firschein, Copeia, 1950, No. 3, Sept., pp. 220-224.

Nos. 2170-2173 adults; nos. 2199-2201 young. This species, formerly recognized under the name *Bufo simus*, is represented by three female specimens, measuring from 24-34 mm. in length, from a mountain just SE of Cañada Grande, 5500 ft. elev. While the characteristic head crests of the young specimens are undeveloped, the parotoid is separated from the eyelid by the narrow width of the incipient supra- or postorbital crest. The species is a new record for the State.

Syrrhophus latodactylus Taylor

Syrrhophus latodactylus Taylor, Univ. Kan. Sci. Bull., vol. 26, 1939 (Nov. 27, 1940), pp. 397-401, pl. 43 and text fig. 7 (type locality, Huasteca Cañon, 15 km. W Monterrey, Nuevo León, Mexico).

A single specimen of this species (no. 2295) is from a point 8 mi. (by road) E of Santa Barbarita, elev. 3400 feet. It was obtained by Mr. S. A. Arny, Apr. 28. The tympanum is subcircular (3 mm. x 2.9 mm.) and approximately three fourths of the length of the eye (4 mm.). There is no trace of vomerine teeth; the flat inguinal gland is present but scarcely discernible except by dissection; a parotoidlike swelling is present above the tympanum. The species has been previously reported from the State.

Hyla eximia Baird

Hyla eximia Baird, Proc. Acad. Nat. Sci. Philadelphia, vol. 7, 1854, p. 61 (type locality, Valley of México, México).

Nos. 2288-2294. Six of the specimens in the collection are from Hacienda Capulín and one from a point 4 miles east (by road) of Santa Barbarita.

Hyla arenicolor Cope

Hyla arenicolor Cope, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 6, 1866, p. 84.

Nos. 2499, 2507 are from 2 km. SW Arriaga.

Hyla miotympanum Cope

Hyla miotympanum Cope, Proc. Acad. Nat. Sci. Philadelphia, vol. 15, 1863, p. 47 (type locality, Jalapa, Veracruz, Mexico [restricted]).

Nos. 2287, 2299-2301. Three male specimens were taken, at a point seven miles east (by road) from Santa Barbarita. These have the tympani a little larger than those in specimens from central and

southern Veracruz. Some fine dark flecks or indefinite reticulations are visible on the dorsum. No. 2787 from the Río Moctezuma, 1 km. S of Tamuzunchale, emphasizes the sharp angular canthus, the sharp folds under the arm and along the inner side of tarsus; and displays a fairly distinct outer tarsal fold also. The skin of the head and to a lesser extent that of the back is strongly corrugated. The choanae are a little smaller than usual and the vomerine tooth series, usually nearly transverse, are slightly diagonal. The throat and breast are milk white, while the remainder of the venter is yellowish white (in preservative).

Other specimens are nos. 2491-2493, El Salto; 2494, 2495, 2 km. SW Huichihuyan.

Smilisca baudinii (Duméril and Bibron)

Hyla baudinii Duméril and Bibron, Erpétologie générale, vol. 8, 1841, pp. 564-565 (type locality, Córdoba, Veracruz [restricted]).

Nos. 2203-2286. This large series of 84 specimens was obtained at the following localities in San Luis Potosí: Capulín; 7 mi. (by road) E of Santa Barbarita; Tamuzunchale; Apetesco (near Xilitla); no. 2498, Valles.

All are males, with paired vocal sacs. The skin of the head is not ossified and is invariably free from the skull. Certain specimens, occurring in northern Mexico, seen elsewhere, have the skin of the head involved in the cranial ossification. I have not been able to ascertain whether this is an occasional condition or whether there is a population having this as a constant character.

Hypopachus cuneus cuneus[9] Cope

Hypopachus cuneus Cope, U. S. Nat. Mus. Bull. 34, 1889, pp. 388-389, fig. 98 (type locality, San Diego, Nueces County, Texas).

Nos. 2318-2351, Hacienda Capulín, collected June 21. A single specimen (no. 2318) is from a point 8 miles (by road) east of Santa Barbarita, taken April 22. Of this series, only four are females.

Rana montezumae Baird

Rana montezumae Baird, Proc. Acad. Nat. Sci. Philadelphia, vol. 7, 1854, p. 61 (type locality, México [city] Distrito Federal, Mexico).

Nos. 2549-2550, Bledos; 2520-2554, 2 km. SW Arriaga; 2521-2538, 2555, 1 km. S Arriaga; 2317, 21 km. E Illescas, 7000 ft. elev.

No. 2554 ♀ is a large melanistic specimen measuring 80 mm.;

[9] The elimination of the subspecific appellation previously used is due to the fact that the southern presumed subspecies S. *baudinii dolomedes* Barbour is actually *Hyla phaeota* Cope.

the dorsal spots can be discerned only with difficulty. The anterior and posterior faces of the thigh are black with fine paper-white dots and flecks. The anterior part of the dorsum has some longitudinal ridges or tubercles, while the posterior part has small tubercles arranged in longitudinal rows. The strong, thick granulation on the sides reaches to the distinct dorsolateral fold.

Other specimens are olive gray and the thighs are light gray with small white spots.

This is the first State record.

Rana pipiens Schreber

Rana pipiens Schreber, Der Naturforscher, Halle, vol. 18, 1872, p. 185, pl. 4 (type locality, Raccoon, Gloucester Co., N. J.).

Nos. 2296-2298 yg., 2303-2316. These series are from the following localities: 1 mi. S Ébano (2303-2306); 7 mi. (by road) E of Santa Barbarita (2307-2308); mountain just SE of Cañada Grande, 5560 ft. elev. (2309-2311); Hda. Capulín (2313-2314); Tamuzunchale (2315-2316); Presa de Guadalupe (2539-2547); Bledos (2548, 2551, 2552); 10 km. E Platanito (2553).

No attempt is made to consider the subspecific relations of this form.

Rana catesbeiana Shaw

Rana catesbeiana Shaw, General Zoology, vol. 3, pt. 1, 1802, p. 106, pl. 33 (type locality, South Carolina [restricted]).

No. 2302. A single specimen taken 1.3 miles south of Ajinche, Apr. 13, by S. A. Arny is the first record of this large species in the State. The snout-vent length is 145 millimeters. The ventral surface is mottled dusky olive-black and yellow-cream, the dark color predominating. The species is already known to occur in Tamaulipas and Nuevo León, so its presence in San Luis Potosí is very probably due to natural range rather than to an importation.

TURTLES

Terrapene mexicana mexicana (Gray)

Cistudo (*Onychotria*) *mexicana* Gray, Proc. Zool. Soc. London, 1848 (1849) pt. 16, pp. 16-17, pl. 2 (type locality, Tampico, Tamaulipas).

Three specimens of *Terrapene* are in the collection, two very typical 4-toed *mexicanus* female specimens and an old 3-toed male. There are numerous differences between the two sexes that suggest that specific as well as sex differences are involved.

Nos. 2477, Taninule; 2478, kilometer 522, Pan-American Highway. These specimens have a high carapace, the scales still dis-

playing growth sculpturing, and the vertebrals except the last, traversed by a narrow, flattened "keel." The edge of the carapace is thin, sharp-edged, and crenellated where it flares out behind. There is still evident a series of elongate yellowish spots tending to form radiating series. The edges of the scales are slightly darkened above, while the plastrons have broad irregular black lines bordering the inner and posterior sutures. The gulars are largely black and the anterior edges of the pectorals are bordered by black. The top of the head is blackish with yellowish spots.

No. 2479 is from the vicinity of Ébano, 4 miles south of Ajinche. In this old male the dorsal scales are smooth, showing no trace of growth lines and the edges of all are heavily bordered with black. Evidence of a flat keel is present on the third and fourth vertebrals. The posterior part of the plastron is thickened, not scalloped or crenellated, while on the sides the edges of the carapace are smoothly rounded, and there is no trace of a sharp edge present. The scales of the arms are definitely smaller, more numerous, and black with yellow centers (male color character). The scales of the plastron, on the other hand, have only narrow borders of black bordering all sutures front and back. The caudal scales are notched, a character not present in the other two specimens. Scales of the under side of the foot are larger and the claws of the hind foot (and to a lesser extent, those of the hand) are much thicker and heavier but not as long as those in the preceding specimens. The outer toe is not free from the integument and there is no trace of a claw on it. A transverse groove on the snout forms a slightly swollen fleshy "nose" above the nostrils. Adequate series of specimens may show that these presumed sexual differences are of specific value.

Kinosternon cruentatum cruentatum Duméril and Bibron

C[*inosternum*] *cruentatum* Duméril and Bibron, in Duméril and Duméril, Catalogue Methodique de la collection des reptiles, livr. 1, 1851, pp. 16-17 (type locality, San Mateo Del Mar, Oaxaca [restricted]).

The discovery in San Luis Potosí of this small three-keeled turtle, known chiefly from southeastern Mexico, in the general region of the Isthmus, extends its known range very considerably northward. The specimen, No. 2480, was taken in an "arroyo 3 miles SSE of Ajinche" in the vicinity of Ébano by Mr. Robert J. Newman, Mar. 15, 1950.

The three keels; the rounded unnotched, unindented, posterior movable part of the plastron; the straight transverse hinges on the movable parts of the plastron; the separation of axillary and inguinal

scutes; the orange or orange-yellow coloring of the plastron, the relatively small size of the species, are characters that refer the specimen to this species.

Kinosternon integrum Le Conte

Kinosternon integrum Le Conte, Proc. Acad. Nat. Sci. Philadelphia, 1854, p. 183 (type locality, Acapulco, Guerrero [restricted]).

A series of five specimens is referred to this species.

Nos. 2481, 2 mi. W. Bledos, 6400 ft.; 2482 Cañada Grande; 2483 San Luis Potosí reservoir; 2485 Hacienda Capulín.

There is considerable difference in the general appearance between nos. 2481, 2482, and the nos. 2483, 2485. The two former have much longer bodies.

LIZARDS

Anolis sallaei Günther

Anolis sallaei Günther, Proc. Zool. Soc. London, 1859, p. 421 (type locality, Jalapa, Veracruz [restricted]).

Under the supposition that *Anolis sallaei* Günther was a synonym of *Anolis sericeus* (Hallowell),* I have previously referred specimens of this species from San Luis Potosí to the latter species. A re-examination of the matter shows that the supraorbital scale rows in *sericeus* are separated by several rows of intercalated scales and the ventral scales are quadrangular. *Sallaei* on the other hand has the supraorbital scales in contact for a part of their length, rarely separated by a single scale row. The occipital scale is separated from the supraorbital scales by rows of three or four scales in *sericeus*, while in *sallaei* it is separated by one or two rows only.

There is a single specimen in the collection (No. 2378) from Río Verde. It is a female, having a slightly longer body than the type. All markings are obsolete.

Ctenosaurus acanthura (Shaw)

Lacerta acanthura Shaw, General Zoology, vol. 3, pt. 1, 1802, p. 216 (type locality, Tampico, Tamaulipas [restricted]).

No. 2415, vicinity of Ébano (1.5 mi. S Ajinche). This specimen, a young female, has the first distinct basal whorl of spines in the tail separated from the second by three scale rows dorsally; the next five whorls by two rows of small scales; next ten whorls by a single row of scales. After these, two rows intervene between the whorls, which now can scarcely be differentiated.

* See Barbour, Bull. Mus. Comp. Zool., vol. 77, 1934, pp. 149-150.

Crotaphytus collaris baileyi Stejneger

Crotaphytus baileyi Stejneger, North Amer. Fauna, No. 3, 1890, p. 103, pl. 12, fig. 1.

One young specimen, No. 2556 from Presa de Guadalupe, is in the collection. There are two complete interorbital scale series, while a third series is not continuous but indicated only by a few small scales. The body has five transverse stripes composed of contiguous, rounded, black spots. The tail is missing and some regeneration has begun.

Phrynosoma orbiculare orbiculare (Linnaeus)

Lacerta orbicularis Linnaeus, Systema Naturae, Ed. 12, vol. 1, 1789, p. 1062 (*part.*).

One specimen, No. 2577, is from near Arriaga.

Phrynosoma modestum Girard

Phrynosoma modestum Girard, *in* Stansbury, Exploration and Survey of the Valley of the Great Salt Lake of Utah, 1852, pp. 361-362, 365, pl. 6, figs. 4-8 (type locality, Las Cruces, New Mexico [restricted]).

No. 2578, 7 km. W Presa de Guadalupe.

Phrynosoma cornutum (Harlan)

Agama cornutum Harlan, Journ. Acad. Nat. Sci., Philadelphia, vol. 4, 1825, p. 299, pl. 20 (type locality, Fort Riley, Geary Co., Kansas [restricted]).

Nos. 2416, 2417. These two road specimens with crushed heads are from the vicinity of Illescas (one from 2 mi. east), at an elevation of 7000 ft.

Holbrookia maculata approximans Baird

Holbrookia approximans Baird, Proc. Acad. Nat. Sci., Philadelphia, 1858, p. 253 (type locality, Tamaulipas, Mexico).

Nos. 2383, 2384, 2 km. E Illescas, 7000 ft. elevation; 2579, 1 km. S Arriaga; 2580-2581, 6 km. NE Arriaga, are referred to this species.

Holbrookia texana (Troschel)

Cophosaurus texanus Troschel, Arch. Naturg., Jahr. 16, vol. 1, 1850 (1852), p. 389, pl. 6 (type locality, New Braunfels, Texas).

No. 2381, Presa de Guadalupe; Nos. 2582-2583, Presa de Guadalupe.

Sceloporus parvus parvus Smith

Sceloporus parvus Smith, Trans. Kansas Acad. Sci., vol. 37, 1934, pp. 263-267, figs. 1, 3, 10 (type locality, Hills 5 miles west Sabinas Hidalgo, Nuevo León).

One badly mutilated specimen, No. 2590, is from Presa de Guadalupe.

Sceloporus variabilis variabilis Wiegmann

Sceloporus variabilis Wiegmann, Herpetologia Mexicana, 1834, p. 51 (type locality, Veracruz, Veracruz, Mexico [restricted]).

Nos. 2382, 2393, 2405. The first two specimens are from 1.3 miles S of Ajinche; the last, from 20 miles NW of Río Verde.

Sceloporus grammicus disparilis Stejneger

Sceloporus disparilis Stejneger, Proc. Biol. Soc. Washington, vol. 29, 1916, pp. 227-230 (type locality, Lomita Ranch, 6 mi. N Hidalgo, Texas).

Two specimens, Nos. 2557 and 2565, are from 3 miles south of San Isidro.

Sceloporus spinosus spinosus Wiegmann

Sceloporus spinosus Wiegmann, Isis von Oken, vol. 21, 1828, p. 370 (type locality, Puebla, Puebla [restricted]).

The following specimens are in the collection: nos. 2390, Cerro Peñon Blanco, 7750 ft.; 2400, mountain just southeast of Cañada Grande; 2404, 1.3 miles W Bledos; 2412, Cerro Peñon Blanco; 2385, 12 miles S Tepetate, 6800 ft.; 2386, mountain just south of Cañada Grande; 2387, San Luis Potosí reservoir.

Sceloporus torquatus melanogaster Cope

Sceloporus melanogaster Cope, Proc. Amer. Philos. Soc., vol. 22, 1885, pp. 400-401 (type locality, Tupátaro, Guanajuato [restricted]).

There are specimens from the following localities in the State: nos. 2388, Mezquitic; 2389, Salinas; 2391, 4 miles NW of Palma, 7800 ft.; 2402, San Luis Potosí reservoir; 2573, 3 km. SW San Isidro. The last specimen is a large, brilliantly colored male, measuring 99 mm. snout-to-vent length.

Sceloporus serrifer plioporus Smith

Sceloporus serrifer plioporus Smith, Zool. Ser. Field Mus. Nat. Hist., vol. 26, 1939 (pub. 445), pp. 212-214, pl. 18, fig. 23 (map) (type locality, four miles E Encero, Veracruz).

Nos. 2574-2575, 10 km. SW Ébano; 2576, 2 km. SW Arriaga; 2392, 1.5 miles south of Ajinche (vicinity of Ébano). This specimen is not typical but agrees with a specimen from El Limón, Tamaulipas, discussed by Smith (*loc. cit.*, p. 213). He suggests that the El Limón specimen may represent an undescribed subspecies of *serrifer*.

Sceloporus jarrovii minor Cope

Sceloporus torquatus minor Cope, Proc. Amer. Phil. Soc., vol. 22, 1885, p. 402 (type locality, Valparaiso Mts., Zacatecas, Mexico [restricted]).

Nos. 2394-2399, San Francisco, vicinity of Alvarez, 6700 ft.; 2401, 7 mi. SSE Cañada Grande; 2403, San Luis Potosí reservoir; 2406, Hacienda Capulín; 2407-2411, 2413-2414, Cerro Peñon Blanco, 7750 ft.; 2558-2564, 2566-2569, 3 km. SW San Isidro; 2570, 2572, 1 km. S Arenal.

Lepidophyma smithi occulor Smith

Lepidophyma smithi occulor Smith, Proc. U. S. Nat. Mus., vol. 92, 1942, pp. 378-379 (type locality, Jalpan, Querétaro, Mexico).

Nos. 2379-2380. Two large specimens, the first measuring 104 mm. snout to vent; tail 107 mm. (partly regenerated); and the second, 100 mm. and 140 mm. respectively. Femoral pores 9-10, and 9-11 respectively. They agree with the type save that the top of the head in both specimens is dark, the sides with two or three light temporal spots. The lower jaw is whitish with three or four dark black spots. These are the only specimens known other than the three in the type series.

Cnemidophorus sackii scalaris Cope

Cnemidophorus gularis scalaris Cope, Trans. Amer. Philos. Soc., vol. 17, pt. 1, p. 47 (type locality, Chihuahua (city) [restricted]).

Nos. 2368-2372. 2 km. east of Illescas, 7000 ft.

These specimens have numerous black irregular transverse bands separated by irregular lines of bluish white or series of bluish white dots, about 24 from shoulder to the base of the tail. The chin and throat are pinkish with a bluish wash, or with a dim spot on each side.

Nos. 2368 and 2371 are referred here with some doubt. The first is a very young specimen; the second a female with distinct longitudinal lines.

Cnemidophorus sackii gularis Baird and Girard

Cnemidorphorus gularis Baird and Girard, Proc. Acad. Nat. Sci. Philadelphia, 1852, p. 128 (type locality, Brownsville, Texas [restricted]).

The following specimens of this common form are in the collection: Nos. 2352-2353, 1.3 miles south of Ajinche; nos. 2354-2358, mountain just east of Cañada Grande, 6400 ft.; no. 2362, 20 kilometers NW Río Verde; nos. 2591-2596, Presa de Guadalupe; no. 2597, 19 km. SW Ébano.

Cnemidophorus sackii communis Cope

Cnemidophorus communis Cope, Proc. Amer. Philos. Soc., 1877, p. 95 (type locality, Colima, Colima).

Several specimens having the characteristics of *C. sackii communis* are referred to this form. It is characterized by the early disappearance of lines and the retention of fine blue dots on a uniform olive or (in preservation) bluish background. The specimens are from the following localities: No. 2359, 1.3 miles west of Bledos; 2361, 1 mile east of La Paz; 2363, Hda. Capulín; nos. 2364, 2365, Salinas. Specimens nos. 2366, 2367, Hernandez, 7800 ft., are believed by Mr. Leslie Burger to exhibit intergrading characters between *C. sackii scalaris* and *C. sackii communis.*

Nos. 2584-2586, 2 km. SW Arriaga; 2587, 1 km. S Arriaga; 2588, 6 km. NE Arriaga; 2589, Bledos.

Barisia imbricata ciliaris (Smith)

Gerrhonotus levicollis ciliaris Smith, Proc. U. S. Nat. Mus., vol. 92, 1942, p. 365 (type locality, Sierra Guadalupe, Coahuila, Mexico).

Nos. 2373 young, 2377 adult, 2 mi. E of Catorce, at Santa Ana mine, 8900 ft. elev.

A gravid female of this subspecies (105 mm. snout to vent), differs from the type in having five large medial supraoculars with 3-2 outer supraoculars; on each side there are four superciliaries in a continuous series. The postmental is divided unequally, and there are 9-10 supralabials. The color is bronze-olive.

A young specimen taken at the same time and place has two small outer supraoculars and a series of six supraoculars, the fifth medial supraocular being reduced in size and having the appearance of a superciliary. Otherwise it agrees in essential details with the preceding specimen.

Eumeces tetragrammus (Baird)

Plestiodon tetragrammus Baird, Proc. Acad. Nat. Sci. Philadelphia, 1858, p. 256 (type locality, Matamoros, Tamaulipas [restricted]).

Nos. 2374, 2376. Two specimens in good condition were taken from the stomach of a hawk, *Buteo magnirostris,* shot 4 miles SSW of Ajinche, on the road to Oviedo, Mar. 18, 1950, by Dr. George H. Lowery, Jr.

The specimens have two pairs of nuchals instead of the more usual three pairs. There are 28 scale rows around the middle of the body.

Eumeces lynxe lynxe (Wiegmann)

Euprepes lynxe Wiegmann, Herpetologica Mexicana, 1834, pp. 36-37 (type locality, El Chico, Hidalgo).

The collection contains a single young specimen (no. 2375) from a "mountain just south of Cañada Grande, S.L.P., 5700 ft. elevation."

SNAKES

Heterodon nasicus kennerlyi Kennicott

Heterodon kennerlyi Kennicott, Proc. Acad. Nat. Sci. Philadelphia, vol. 12, 1860, pp. 336-337 (type locality, Brownsville, Texas [restricted]).

No. 2420, 2 km. E Illescas, 7000 ft. The following characters obtain in the specimen: four accessory scales on snout; ventrals 143; anal divided; subcaudals 27 (the tail incomplete); scale rows 23-23-21-19; pre-post-subocular series, 10, 8.

Ninia diademata plorator Smith

Ninia diademata plorator Smith, Copeia, 1942, pp. 153-154 (type locality, Durango, Hidalgo).

This is the northernmost record for the genus, and the first record for San Luis Potosí. No. 2602, a female, has a ventral count of 133, and a subcaudal count of 81 + 1. The supralabials are 6-6 and there are but two pairs of chinshields. Total length 255 mm.; tail 83 mm.

Dryadophis melanolomus veraecrucis Stuart

Dryadophis melanolomus veraecrucis Stuart, Misc. Publ. Mus. Zool. Univ. Michigan, no. 49, 1941, pp. 91-93, pl. 4, fig. 6, map 4 (substitute name for *mexicanus*) (type locality, Zacuapán, Veracruz).

No. 2431, vicinity of Xilitla, at Apetsco.

Elaphe emoryi emoryi (Baird and Girard)

Scotophis emoryi Baird and Girard, Catalogue of North American Reptiles, 1853, pp. 157-158 (type locality, Howard Springs, Texas).

Nos. 2418 ♂, 2419 ♀, 1½ miles S Ajinche, vicinity of Ébano. The species, previously known in the State from a single specimen taken at Ébano, is represented by two more from the same general area.

The specimens, respectively, present the following scale data: Scale row formulae 25-27-25-19, 25-27-23-19; ventrals 233, 235; subcaudals 68 + 1, 65 + 1; anals 2, 2; dorsal body blotches 34, 37; tail blotches, 14, 13.

Lampropeltis getulus splendida (Baird and Girard)

Ophibolus splendidus Baird and Girard, Catalogue North American Reptiles, pt. 1, p. 83, (type locality, Santa Rita Mts. [restricted]).

No. 2421, vicinity of Illescas, 7000 ft. The finding of a specimen of this subspecies far south of the known range is indeed a surprise since the characteristics maintained are those of the typical specimens.

Laterally the black scales bear yellow dots, the size of the dots varying so as to produce an indefinite pattern of very narrow dark and light diagonal lines. The scales of the dorsum are black but at intervals one to four small yellow dots placed transversely break the black area into 56 incompletely delineated spots or bands. The venter is coal black, with each ventral scale bearing a large white dot at one end or the other; or not impossibly, on both ends. The anal scale is white. The head is coal black save for some indefinite yellow marks on the scales of the snout and labials, the lower labials and chinshields each bearing a yellow spot. The following characters obtain: length 437 mm.; tail 65 mm.; scale rows 23-23-23-19 (33 rows about back of head); ventrals 203; subcaudals 53 + 1; anal single; supralabials 8-8, infralabials 9-9.

The nearest point where specimens of this form have been taken previously, is the lower Rio Grande valley in Texas, a distance of nearly three hundred miles. In Mexico, it has been reported previously in northern Chihuahua and (questionably) northeastern Sonora. This is a most interesting addition to the known range of the species.

The specimen was obtained by Mr. Robert Newman.

Masticophis flagellum lineatulus Smith

Masticophis flagellum lineatulus Smith, Journ. Washington Acad. Sci., vol. 31, 1941, pp. 394-397 (type locality, 11 miles south of San Buenaventura, Chihuahua).

Three specimens of this very distinctive subspecies are present in the collection: no. 2422 from the vicinity of Illescas, 7000 ft.; no. 2423, 2 kilometers east of Illescas, 7000 ft.; no. 2424, Hernandez. The scale counts for the three specimens are:

Number	Ventrals	Anals	Subcaudals
2422	193	2	48 +
2423	194	2	69 +
2424	192	2	103

The brilliant pink or salmon-pink coloration of much of the ventral surface is a conspicuous feature of this form. The throat and chin are heavily mottled in brown, the spots tending to coalesce. Paired

spots on the anterior ventrals are brown with often a pinkish center, which in some cases increases until only a tiny black spot of the dark color is left.

Masticophis flagellum testaceus (Say)

Coluber testaceus Say, in Long's Expedition to the Rocky Mountain, vol. 2, 1823, p. 48 (type locality, Pueblo, Colorado [restricted]).

Three specimens are in the collection: no. 2428 ♂, Laguna Chica, vicinity of Ébano; no. 2598, 12 km. SE Presa de Guadalupe (a large, badly mutilated road specimen); no. 2599, 28 mi. S Matahuala.

The scale counts are: 2428, ventrals 192, subcaudals 109 + 1; 2598, ventrals 202, subcaudals 103 + 1; 2599, ventrals 200, subcaudals 104 + 1.

No. 2599 is represented by a skin including the head and tail intact. It differs markedly from the two other specimens in having six light, broad, irregular bands (or blotches) separated by dark bands on the anterior half of the body. At a point near the middle, the bands cease. There are some small dark dots or flecks scattered on the light bands.

This unusual variety is noted by Ortenburger in his monograph, Whipsnakes and Racers (Univ. Michigan Press, 1928, p. 94), but localities are not given.

Drymarchon corais erebennus (Cope)

Spilotes erebennus Cope, Proc. Acad. Nat. Sci. Philadelphia, vol. 12, 1860, p. 342 (type locality, Eagle Pass, Texas).

No. 2600, 19 km. SW Ébano. The specimen has 181½ ventrals and 61 + 1 subcaudals.

Pituophis deppei jani Cope

Pituophis jani Cope, Acad. Nat. Sci. Philadelphia, vol. 12, 1860 (1861), p. 369 (type locality, Buena Vista, Coahuila).

No. 2425. This specimen, from 15 kilometers NW of San Luis Potosí, has the anterior blotches entirely black, while the more posterior blotches still show some brown about the bases of the individual scales, the greater portion of each scale being black. There are 29 black spots on the body and 9 on the tail. The light intervening spots are five or six scales long. The scales of the venter number 227, the anal is single, and the subcaudals 58. In the number of the spots, the species is a typical *jani;* in the tendency for

the light interspaces to be reduced to four and three scale-lengths, it approaches *deppei.* In the tendency for the brown posterior spots to become black the approach is toward *deppei.* Scale counts are not definitive since they are in the overlapping range. The tendency for the dorsal spots to fuse on the sides, points to *jani.* The locality, however, is in an area where intergradation is to be expected; but since the greater number of characters are those of *jani,* I have referred it to this form.

No. 2603 is a young specimen from 15 mi. NE of San Luis Potosí (city). Ventrals 218, subcaudals 60 + 1. There are 28 blotches. The head is very light with markings very faintly indicated.

Pituophis sayi affinis Hallowell

Pituophis affinis Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1852, p. 181 (type locality, Zuñi, New Mexico [restricted]).

Two specimens of a *Pituophis,* one from 2 kilometers east of Illescas, 7000 ft. (no. 2426), and the other from the vicinity of Illescas (no. 2427) are referred to this subspecies. It is from a locality considerably south of the previously known range. The specimens, while not agreeing in all detail with the more typical *affinis,* do agree in most characters and patterns.

The specimens have the following scale counts:

Number	Body spots	Tail spots	Ventrals	Subcaudals	Scale formula
2426	38	13	220	60 + 1	31-29-31-21
2427	45	15	215	66 + 1	31-29-31-23

The color of the head is gray to tan-olive with a series of small irregularly placed black spots on the posterior head scales (frontal and occipital regions), and the labials are bordered by narrow vertical lines of black. The dorsal spots are brown anteriorly, becoming somewhat reddish or reddish brown. The skin is brownish red between the scales. On the tail the skin between the scales forming the spots is red while the scales themselves are brownish red. The chin and throat are immaculate white.

Thalerophis mexicanus mexicanus (Duméril, Bibron and Duméril)

Leptophis mexicanus Duméril, Bibron and Duméril, Erpétologie Générale, vol. 7, pt. 1, 1854, pp. 536-537 (type locality, Potrero Viejo [restricted]).

No. 2437. A single specimen of this well-known species was taken 15 kilometers east of Ébano by Mr. W. Dalquest. The ventrals number 170; anals 2; subcaudals 161 + 1.

Tropidodipsas sartorii sartorii Cope

Tropidodipsas sartorii Cope, Proc. Acad. Nat. Sci. Philadelphia, vol. 15, 1863, p. 100 (type locality, Mirador, Veracruz).

No. 2429. One road specimen was obtained three kilometers north of Valles. The color of the specimen was "dark purple and pale orange bands."

Natrix rhombifera blanchardi Clay

Natrix rhombifera blanchardi Clay, Ann. Carnegie Mus., vol. 27, 1938, pp. 251-253, pl. 25 (type locality, Tampico, Veracruz [restricted]).

No. 2432. 6 km. N Tamuín. The specimen has the ventral surface much clouded on the ends of the ventrals, while on the tail there are discrete black triangular subcaudal spots. The ventrals number 143, anals 2, subcaudals 86. The head is dark, almost black, and the dorsal pattern is obscure unless the specimen is submerged.

Thamnophis eques eques (Reuss) Smith

Coluber eques Reuss, Mus. Senckenberg. Abh., vol. 1, 1834, p. 152, pl. 8, fig. 2 (type locality, Mexico).

A very young specimen, no. 2434, from Santa Teresa, and an adult, no. 2601 from Bledos are in the collection. The latter specimen has the following scale count: ventrals 162, subcaudals 69.

Thamnophis sirtalis proximus (Say)

Coluber proximus Say, *in* Long's Expedition to the Rocky Mountains, vol. 1, 1823, p. 187 (type locality, three miles above the mouth of Boyer's River, stonequarry on west side of Missouri River, Washington Co., Nebraska).

Nos. 2435, 2436 from 6 km. N Tamuín.

Storeria dekayi texana Trapido

Storeria dekayi texana Trapido, Amer. Midl. Nat., vol. 31, 1944, pp. 63-70, figs. 45-50 (type locality, Edge Falls, 4 miles south of Kendalia, Kendall Co., Texas).

No. 2430. The single road specimen in the collection from Xilitla, does not permit absolute identification as to subspecies, since the head scales are largely destroyed. It is in the known range of this subspecies.

Storeria storerioides (Cope)

Tropidoclonium storerioides Cope, Proc. Acad. Nat. Sci. Philadelphia, vol. 17, 1865, pp. 190-191 (type locality, Tres Cumbres, Morelos [restricted]).

No. 2433. A single secimen of this widely distributed form is in the collection from a mountain just south of Cañada Grande, 5700 ft. elev.

Bothrops atrox asper (Garman)

Bothrops atrox asper Garman, Bull. Mus. Comp. Zool., vol. 8, 1883, p. 124 (type locality, Obispo, Panamá).

No. 2444 is a headless specimen from the vicinity of Xilitla.

Crotalus lepidus lepidus (Kennicott)

Caudisonia lepidus Kennicott, Proc. Acad. Nat. Sci., Philadelphia, vol. 13, 1861, p. 206 (type locality, Presidio del Norte, Texas [restricted]).

A single specimen of this species was taken at Cerro Peñon Blanco, 9600 feet.

Crotalus atrox Baird and Girard

Crotalus atrox Baird and Girard, Catalogue of North American Reptiles in the Museum of the Smithsonian Institution. Pt. 1. Serpents. 1853, p. 5 (type locality, Indianola, Texas [restricted]).

The following specimens of this species were taken: Nos. 2439, Hacienda Capulín; 2440, vicinity of Illescas, 7000 ft.; 2441-2443, 2 miles E of Illescas, 7000 ft.

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Taxonomy and Distribution of the Horned Lizard Genus *Phrynosoma*

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ABSTRACT: The lizards of the genus *Phrynosoma* are treated monographically. Fourteen species are recognized with a total of 27 forms (species and subspecies). Considerable information is given on taxonomic history, osteology, habits, and speciation. A series of maps give a complete picture of the known distribution of each form. No new names are proposed, but one name, *Phrynosoma platyrhinos calidiarum*, is revived.

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INTRODUCTION

In reviewing the genus *Phrynosoma* taxonomically, I have sought to determine and describe the existing species and subspecies, provide ready means for recognizing the named forms, and to map the geographic distribution, as now known of each kind. Whether some named forms should be lumped together or whether additional variants should be described as new, had to be decided. This was done mostly on the basis of the worker's knowledge and his interpretations of the available data. Even so, personal opinion played some part. Questions that arose concerning the relationships of one form to another included the following: Were certain forms that lived in areas adjacent to each other species or subspecies? What were the characters that could be depended upon to show the true relationships of the kinds of lizards involved? It was soon found that no single set of criteria would suffice; characters that showed relationships of taxonomic worth in one case, seemed not to do so in another. In some instances various characters were given numerical "weights" which were recorded and the total weight of the characters for each kind of lizard was computed. In this

manner the different forms of lizards could be arranged in a definite sequence. Whether this is indicative of their true relationship might be questioned. However, when lizards were arranged by the "weight" system, the arrangement corresponded closely to the arrangement arrived at by other less exact means of estimating relationships of the same lizards. The maintenance of a constant attitude toward similar problems has been attempted throughout the paper.

METHODS AND MATERIALS.—I have attempted to make all the synonymies complete. However, in some instances it has been impossible to relegate positively each reference to its proper place owing to my inability to determine what species was being treated by the author. In such an instance placement was made in accordance with my own idea as to probability.

The descriptions have been made from a series of specimens where such were available and the average conditions of each character was recorded as if present on a single specimen. Under the topic variation, only a few characters that I consider salient have been discussed. It must be realized that more characters than those mentioned also vary. The descriptions of color and color pattern are from alcoholic specimens submerged in water.

Twenty-two measurements and twenty-one other items of data were recorded from each specimen handled. The measurements were made with a vernier caliper and all were taken by myself to assure as much uniformity as possible. The measurements found to be of most significance in this study are as follows:

Total length	= tip of snout to tip of tail.
Snout-vent	= tip of snout to posterior edge of anal flap.
Tail length	= posterior edge of anal flap to tip of tail.
Arm length	= pit of arm to tip of longest finger exclusive of claw.
Leg length	= insertion of leg with body to tip of longest toe, exclusive of claw.
Head length	= tip of snout to posterior edge of skull between occipital spines or at the base of interoccipital spine if present.
Head width	= width across the angles of the lower jaws.
Frontal width	= widest part of frontal area, exclusive of superciliary spines.
Eye-snout	= tip of snout to anterior edge of eyelid.
Eye-ear	= ventral extent of eyelid to dorsal edge of auricular opening.
Ear-snout	= tip of snout to anterior edge of one auricular opening.
Spine length	= tip of spine to base of spine.

Combinations of these measurements were computed as ratios and set up as indices by the sample formula, $\Sigma \left(\frac{\text{snout-vent}}{\text{total length}} \times 100\right) =$ average ratio in percentages where a series of specimens was avail-

able. The actual measurements of individuals are given in the species of which only a few specimens were available.

The nomenclature used in the descriptions is mainly that of Smith (1946, Handbook of Lizards). For characters or structures not named in Smith's book, I have applied the names which have general acceptance.

The abbreviations used in the locality data are as follows:

AMNH	American Museum of Natural History
USNM	United States National Museum
MVZ	Museum of Vertebrate Zoology, University of California.
LMK	Private collection of Dr. Laurence M. Klauber
SSNH	San Diego Society of Natural History
BYU	Brigham Young University
UU	University of Utah
NSM	Nebraska State Museum, University of Nebraska
KU	University of Kansas Museum of Natural History
EHT-HMS	Private collection of Dr. Edward H. Taylor
STANFORD	Leland Stanford Jr. University

The photographs, in the main, were made by the University of Kansas Photography Laboratory.

The maps portray only the general areas in which the species or subspecies might be expected to occur. Naturally the populations are continuous only in those areas favorable for *Phrynosoma*. The boundaries of the species are based upon the known distribution of the species and also on the geography of the adjacent areas.

ACKNOWLEDGMENTS.—It has been only through the generous loan of books, specimens, and information by a number of individuals and institutions that my study was completed. I thank Prof. Vasco M. Tanner for suggesting and helping me initiate the problem as well as for lending to me the collection at Brigham Young University; Prof. Alden H. Miller and Prof. Robert C. Stebbins at the Museum of Vertebrate Zoology, University of California, for their hospitality while I was there, as well as for the loan of part of the extensive collection in their charge; Dr. Laurence M. Klauber for the loan of his personal collection and that of the San Diego Society of Natural History; Miss Margaret Storey, Stanford University, for making available the collection there; Prof. Angus M. Woodbury of the University of Utah for the loan of the collection of that University; Dr. Doris M. Cochran at the United States National Museum for making available their large collection, for supplying a place to work and allowing me to use the library facilities while at the Museum; Mr. Charles M. Bogert of the American Museum of Natural History for making

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CLASSIFICATION OF THE GENUS *PHRYNOSOMA*

Class Reptilia Laurenti
Subclass Diapsida Osborn
Order Squamata Oppel
Suborder Sauria Macartney
Family Iguanidae Gray

Genus *Phrynosoma* Wiegmann

Lacerta (*part.*) Linnaeus, Systema Naturae, 12 ed. vol. 1, 1766, p. 365-366.
Cordylus (*part.*) Laurenti, Specimen Medicum, exhibens synopsin Reptilium . . ., 1868, p. 56.
Tapaja (*part.*) Oken, Lehrbuch der Naturgeschichte, dritter Theil, Zoologie zweite Abteilung, Fleischthiere, Jena, 16, 1816, p. 294.
Tapayia Gray, Ann. Philos., NS., vol. 26, 1825, p. 197.
Tapaya (*part.*) Fitzinger, Neue Classification der Reptilium. Wien., 1926, p. 17.
Phrynosoma Wiegmann, Isis von Oken, 1828, p. 367.
Batrachosoma Fitzinger, Systema Reptilium, 1843, p. 79.
Tropidogaster Fitzinger (*nec.* Duméril & Bibron) (*loc. cit.*)
Anota Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1852, p. 182.
Doliosaurus Girard, United States Exploring Expeditions of the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes USN, vol. 20, 1858, Zoology, p. 407.

TAXONOMIC HISTORY

Linnaeus (1766) described from the work of Seba (1734) the species *Lacerta orbicularis.* In this description Linnaeus distinguishes an α and β form. The form α is based upon the reference "*Mus. Ad. Fr.* I. P. 44. Lacerta eadem," and "*Seb. Mus.* I. t. 109. f. 6., t. 83. f. 1, 2." The form β is based upon "*Seb. Mus.* I. p. 134. t. 83. f. 1, 2, Lacerta orbicularis spinosus; *Hern. Mex.* 327, 328, Lacertus orbicularis; *Raj.* quadr. 263, Lacertus orbiculatus."

Two years later Laurenti, (1768, p. 51) restricted the Linnaean name by referring Seba's plate 83, figs. 1, 2, to *Cordylus orbicularis,* while basing the name *Cordylus hispidus* on Seba's plate 109, fig. 6. Inasmuch as figs. 1 and 2 of pl. 83 in Seba are reproduced from Hernandez, libr. 9 C. 16, the proper restriction of Linnaeus' name

to the Mexican species commonly known as *Phrynosoma orbiculare* is assured.

There are three available names antedating the Wiegmannian name *Phrynosoma* that must be considered. The first is *Tapaja* (1816, p. 294, Index p. 1266, erroneously spelled *Tapaia* in the table of contents, p. 6). Oken used the name in a subgeneric sense, under the genus *Agama*. The trivial names referred to *Tapaja* are not used with that generic name but with *Agama*. The first species cited under *Tapaja* is *Agama orbicularis* (Linnaeus, presumably, although no author is cited). Other species mentioned are *Agama plica* and *Stellio helioscopus*. Oken's inconsistency in the usage of generic names and failure to cite the origin of trivial names is very confusing.

The next name in chronological order is *Tapayia* Gray (1825, p. 197). This subgenus was cited with the single species *Lacerta orbicularis* Linnaeus.

The third name, *Tapaya* Fitzinger (1826, p. 7) included three species: *T. orbicularis* Cuvier, *T. gemmata* Cuvier, and *T. deserti* Fitzinger.*

The generic name *Phrynosoma* was proposed by Wiegmann in his "Beytrage zur Amphibienkunde" in Isis von Oken 1828, p. 367. Four species are there considered, as belonging to the genus: "*P. orbiculare* [*L. orbiculare* Linnaeus], *P. bufonium*, Wieg. *P. gemmata* and *P. cornutum* [*Agama cornuta* Harlan]."

Wiegmann (1834, p. 52) defines the genus as follows:

"*Caput* breve, postice valde dilatatum spinarum validarum corona cinctum, irregulari-tetraëdrum, fronte plana, clypei ad instar supra orbitas adscendente.

"*Dentes* maxillares parvi, simplices, cylindrici, obtusi, conferti, aequales; primores 5. Palatum edentulum.

"*Aures* apertae, sub colli plicis absconditae, tympano altius detruso.

"*Lingua* crassa, apice incisula. *Nares* anticae.

"*Truncus* compactilis, ovalis, depressus, bufonius, superne squamis inaequalibus, minutis vestitus, aliisque maioribus, acutis, sparsis spinulosus, ad latera aculeorum serie fimbriatus.

"*Cauda* brevis, basi latissima, depressa, apice teretiuscula, squamis imbricatim vestita.

"*Membra* pro corporis mole breviuscula.

* The above was taken in part from Smith & Reeve, Herpetologica, vol. 7, pt. 2, 1951, pp. 53-55.

"*Glandularum* femoralium pori parum conspicui."

Wiegmann did not designate a type species.

Fitzinger (1843) divided the genus into three subgenera: *Phrynosoma* containing *P. orbiculare* Wieg. (Linnaeus) and *P. douglassii* Wiegmann (Bell); *Batrachosoma* with *P. coronatum blainvillii;* and *Tropidogaster* with *P. cornutum* Gray (Harlan), and *bufonium* Wiegmann (*P. cornutum* (Harlan)). In this same work (page 17) he designates *P. orbiculare* Wiegmann (Linnaeus), as the type species of Wiegmann's *Phrynosoma.* Girard (1858) revised this genus dividing it into four subgenera two of which (*Phrynosoma* and *Batrachosoma*) were taken directly from Fitzinger (*op. cit.*), and a third (*Tapaya*)† from Cuvier (1817) and a fourth (*Doliosaurus*) being new. Under *Phrynosoma* Wiegmann, he placed *P. cornutum* Gray (Harlan) and *P. regale* Girard = (*P. solare* Gray). Under *Batrachosoma* Fitzinger appeared *B. coronatum* Fitzinger = [*P. coronatum coronatum* Blainville (*part.*), *P. c. blainvillii* Gray (*part.*), *P. c. frontale* Van Denburgh (*part.*) and *P. solare* Gray (*part.*)]. In *Tapaya* Cuvier, he places *T. orbicularis* Cuvier = (*P. orbiculare orbiculare* Linnaeus), *T. hernandesi* Girard = (*P. douglassii hernandesi* Girard), *T. ornatissimum* Girard = (*P. d. ornatissimum* Girard), *T. brevirostris* Girard = (*P. d. brevirostre* Girard) and *T. douglassii* Girard = [*P. d. douglassii* (Bell) (*part.*) and *P. d. ornatum* Girard (*part.*)]. Girard (1858) had divided *P. douglassii* into two distinct species assigning the name *P. ornatum* to the second. Before publication of the work, however, he changed his mind, and retained them both in the former species with the comment that "two species may yet be confounded under this heading . . . , all specimens from the northwest coast are much smaller than those of the more southern region of Utah; but since this fact might still be regarded by some as bearing upon the climate, we have, so far, refrained from recording them as distinct species." However, the plates for the work had been completed and processed by this time, resulting in the figure of this form carrying the caption *P. ornatum.* In the text *P. ornatum* is in the synonymy of *P. douglassii.* In his fourth subgenus *Doliosaurus,* Girard placed *D. mc'calli* Girard = [*P. platyrhinos platyrhinos* Girard (*part.*) and *P. p. calidiarum* (Cope) (*part.*)], and *D. modestus* Girard = (*P. modestum* Girard). Girard supplied the name *Doliosaurus* instead of using *Anota.* His reason for not using the latter was that the name typified only one of the three genera he wished to

† Cuvier, Reg. Anim. vol. 2, 1817, p. 55, refers to the group as "les Tapayes" he does not use the term as a scientific name.

place under it, and not that it was preoccupied as indicated by Cope (1900). Aug. Duméril and Bocourt (1870) and Bocourt (1874) retain the Girardian subgenera *Phrynosoma, Tapaya,* and *Batrachosoma* substituting Hallowell's *Anota* for Girard's *Doliosaurus.* The arrangement of the species under these subgenera varies from that of Girard only in the case of *Anota* where only *A. mc'callii* Hallowell is included. Duméril and Bocourt place *modestum* and *platyrhinos* in the subgenus *Phrynosoma.*

Cope (1900) considered the group of species as two distinct genera: *Phrynosoma* and *Anota.* He defines the latter with the statement, "This genus only differs from *Phrynosoma* in the concealment of the tympanic drum by the integument, which is scaly." In this genus he placed five species (four according to his text): *A. modesta* Girard = (*P. modestum* Girard), *A. calidiarum* Cope = (*P. platyrhinos calidiarum* Cope), *A. goodei* Stejneger = (*P. platyrhinos goodei* Stejneger), *A. platyrhina* Girard = [*P. platyrhinos platyrhinos* Girard (*part.*) and *P. d. calidiarum* Cope (*part.*)] and *A. maccallii* Hallowell = (*P. m'callii* (Hallowell). The character used by Cope to define this genus was recognized by Girard (1858) to be of a variable nature in two of the three species he wished to place under it. This led to his usage of the subgeneric name *Doliosaurus* rather than *Anota.* Cope's arrangement was therefore not popularly followed. Bryant (1911) in working with the California species of the genus also placed *m'callii* in the genus *Anota,* based upon the apparent closure of the supratemporal fossae by bone. His observations, however, were based upon a single specimen and because of this, his arrangement was not generally followed. Van Denburgh (1922) recognized only *Phrynosoma* as did Smith (1946). I have here recognized only the genus *Phrynosoma.*

OSTEOLOGY

The descriptive osteology given here is based mainly upon the skeleton of the species *Phrynosoma cornutum.* Cope (1900), Bryant (1911) and Broom (1948) are drawn upon freely throughout the descriptions.

Premaxillary: The premaxillary bone is at the apex of the upper jaw. It is approximately one to one and one-half times as high as wide. Dorsally it forms a wedge between the paired nasal bones, which overlap it laterally. The premaxillary bone forms only a small part of the boundary of the nasal openings, articulating dorsally with the nasals and laterally with the maxillaries.

Nasals: The nasals flank the posterior part of the fused premaxillaries extending posteriorly and laterally where they meet the frontals and prefrontals. The nasals form the medial and most of the dorsal boundary of the nasal openings.

Prefrontals: The prefrontals are roughly crescent-shaped and lie laterally and posteriorly to the nasals. Anteriorly they complete the dorsal and lateral part of the boundary of the nasal opening articulating there with the nasals and the maxillaries. A lateral posterior projecting process forms the anterior half of the superciliary bar. Posteriorly the prefrontals articulate with the frontals.

Frontals: The frontal bones are fused into a single element, which is roughly T-shaped. The anterior part forms a wedge between the prefrontals and articulates with the nasals. The posterior border forms with the parietals a nearly straight transverse suture, which passes through the pineal foramen. The anterior and lateral projections of the frontal form the posterior half of the superciliary bar. The frontal and prefrontals form the entire boundary of the superciliary fossae.

Postorbital: The postorbital forms the posterior boundary of the orbit articulating dorsally with the frontal and parietal, and ventrally with the jugal and squamosal. The postorbital may bear several tubercles.

Parietals: The parietals are fused, forming the heavy posterior, medial border of the head where it supports two large lateral and one small medial occipital spines. The parietal articulates anteriorly with the frontals, laterally with the postorbital, squamosal, tabulare and opisthotic, and posteriorly with the supraoccipital, and prootic. Its surface is covered with numerous tubercles.

Squamosal: The squamosal bones form the posterior lateral angles of the skull articulating medially with the parietal, tabulare, quadrate, and opisthotic and laterally with the jugal and postorbital. It bears laterally three moderately large spines and forms with the postorbital and parietal the boundary of the supratemporal fossa.

Jugal: The jugal articulates posteriorly with the squamosal, dorsally with the postorbital and anteriorly with the maxillary. The jugal forms the central portion of the ventral border of the optic cavity. Medially it articulates with the ectopterygoid.

Paraoccipitals: The paraoccipitals furnish the lateral lobes of the occipital condyle, articulating ventrally with the basioccipital, laterally with the opisthotic, dorsally with the supraoccipital and anteriorly with the prootic.

Maxillary: The maxillary completes the bones of the lateral part of the skull. It articulates posteriorly with the jugal and anteriorly with the premaxillary. A dorsal projection meets the prefrontal at the dorsolateral corner of the nasal opening. The maxillary forms the ventral and lateral boundary of the nasal opening. Medially it articulates with the palatine.

Basioccipital: The basioccipital furnishes the central part of the tripartite condyle. It articulates dorsally with the paraoccipitals, and anteriorly with the basisphenoid.

Supraoccipital: The supraoccipital articulates ventrolaterally with the opisthotic, dorsally with the parietal, and forms the upper boundary of the foramen magnum.

Opisthotic: The opisthotic articulates medioventrally with the basioccipitals, laterally with the tabulare, quadrate and parietal, anteriorly with the prootic, and forms the lateral boundary of the foramen magnum.

Tabulare: The tabulare is a small thin bone, wedged between the opisthotic, squamosal, quadrate and the parietal.

Prootic: The prootic can be seen through the fossa formed by the opisthotic, supraoccipital and parietal. The prootic articulates dorsally with the parietal and ventrally wih the supraoccipital, paraoccipitals and opisthotic.

Quadrate: The quadrate bone is troughlike in appearance, and the hollow area is directed posteriorly. The bone articulates dorsally with the squamosal, tabulare, and parietal bones, extending ventrally and slightly anteriorly to form at its ventral end the articulating surface that receives the articulare of the lower jaw. Medially and toward the distal end the quadrate articulates with the pterygoid.

Basisphenoid: The basisphenoid forms a broad triangle if the pterygoid processes are omitted from consideration and articulates posteriorly with the basioccipital by means of a nearly straight suture and laterally with the pterygoid by means of the pterygoid process. An anterior membranous projection of the basisphenoid articulates with the medial edges of the palatines.

Pterygoid: The laterally compressed posterior part of the pterygoid articulates with the medial distal end of the quadrate. The central part articulates mesially with the basisphenoid, laterally with the ectopterygoid and dorsally with the epipterygoid. The anterior dorso-ventrally compressed part articulates anteriorly with the prevomer and medially by cartilage with the projecting spine of the basisphenoid.

Ectopterygoid: The ectopterygoid is a short bone extending from the mediolateral process of the pterygoid to the suture of the jugal and maxillary of the upper jaw.

Epipterygoid: The epipterygoid extends dorsally and posteriorly from the middle part of the pterygoid to the bottom of the prootic bone. The epipterygoid is characteristic in that it does not reach the parietal as is the case in other lizards.

Palatines: The palatines are without teeth and extend posteriorly from the pterygoids, which they overlap slightly, to the prevomers. The palatines articulate laterally with the maxillaries.

Prevomers: The prevomers articulate anteriorly with the premaxillaries, laterally with the ventral process of the prefrontals, and posteriorly with the palatines. The prevomers meet at their anterior extremities for a short distance but are separated for most of their length by a hiatus.

Stapes: The stapes is long and slender, extending from the capsul at the base of the opisthotic ventrolaterally to where it abuts against the tympanum. The stapes apparently does not receive additional support from the quadrate, as is the case in some other groups of lizards.

Dentary: The dentary comprises the anterior half of the lower jaw, and bears all of the incisorlike teeth. On the lateral surface it articulates posteriorly with the small dorsally located coronoid and the large surangulare. Medially the dentary is split about midway into two rami. The ventral ramus articulates first with the splenial and more posteriorly with the narrow angulare.

Surangulare: The surangulare makes up the posterior half of the lateral surface of the jaw, bearing on its ventrolateral margin from four to six protuberances that increase in size from front to back. The surangulare articulates on the anterolateral surface of the jaw with the dentary and coronoid, and on the posterolateral surface with the articulare and prearticulare. Ventrally the surangulare articulates with the dentary and the angulare and medially with the prearticulare and coronoid.

Articulare and Prearticulare: The articulare is fused with the prearticulare. They articulate laterally with the surangulare, ventrally with the angulare, and medially with the splenial and coronoid.

Angulare: The angulare is small and somewhat spindle-shaped, seen best from the ventromedial angle. The angulare is bordered medially by the prearticulare and the splenial and laterally by the dentary and the surangulare.

Splenial: The splenial bone is on the inner surface of the jaw forming, with the anterior projection of the coronoid, the wedge that fits between the two rami of the dentary. The splenial articulates anteriorly with the dentary and coronoid and posteriorly with the angulare and prearticulare.

Coronoid: The coronoid bone forms the dorsal projection or bump on the mandible and articulates laterally with the dentary and surangulare and medially with the dentary, splenial, prearticulare and the surangulare.

Vertebral column: The vertebral column consists of approximately 31 procoelous vertebrae, bearing ribs from the third to the twenty-second inclusive. The two sacral vertebrae are partly fused. The neural spines are short. The haemal arches are present on from six to eight caudal vertebrae, being rudimentary or vestigial on the remaining. The vertebrae lack the zygosphene articulation although corresponding rudimentary processes are present. Intercentra are present only in the cervical vertebrae.

Ribs: There are usually twenty pairs of ribs, of which the first pair and the last four or five pairs are short, the second to seventh articulating by cartilage with the sternal ribs.

Pectoral girdle: The sternum is large and about as wide as long. A large foramen pierces the posterior half. The front angle is acute, (55°-60°), with the sides grooved to receive the coronoid bones. The posteriorlateral margins are serrate, each point being the articulating surface for a sternal rib of which there are two in this species. The ziphoid processes articulate at the posterior angles of the sternum and join the cartilage of the eighth pair of ribs.

Interclavicles: At the anterior tips of the sternum are found the slightly curved laterally projecting interclavicles. The clavicles meet each other medially where they articulate with the anterior dorsal surface of the medial portion of the interclavicles. Distally the clavicles are in contact with the anterior edges of the scapula and suprascapula.

Coracoid: The coracoid is in broad contact with the sternum and projects anteriorly beneath the clavicle and interclavicle where, with a process from the scapula, it forms two separate foramina. The foramina may be open on the anterior edge in young specimen.

Scapula: The scapula is about equal in length to the coracoid, but is considerably narrower. The suprascapula is nearly twice as long as the scapula, curves posteriorly and lies upon the ribs.

Pelvic girdle: Ilia: The ilia are stout, extending obliquely dorso-

caudally. The inner side of the anterior dorsal border articulates with the pelvic ribs.

Pubes: The pubes are unevenly curved, and differ from the ilia in being lighter structurally and slightly longer.

Ischia: The ischia are intermediate in weight between the ilia and pubes and are longer than either. Both the pubes and ischia lie in the transverse plane and are connected medially by a thin cartilaginous rod. They form two large ischiopubic foramina. A cartilaginous rod projects posterodorsally from the median symphysis of the ischia.

Limbs: The limbs are typically lacertilian in structure.

FEEDING HABITS

Examination of the stomach contents of a number of these lizards shows the preferred food to be insects of which the greatest percentage is ants. The myrmecophagus diet is not surprising when it is realized that ants occur in abundance throughout the areas inhabited by the horned lizards. I doubt, however, that the absence of ants from an area would alone prohibit the occurrence of these lizards, if other ground living insects were present. In Utah, Knowlton and Jones (1934:10) and Knowlton and Thomas (1936:65), found by stomach examination that these lizards ate a variety of insects, including beetles, grasshoppers, weevils, and leafhoppers. I have successfully kept alive, in captivity, specimens of *P. d. ornatissimum* and *P. cornutum,* by feeding them crickets, blister beetles, woodborer larvae, centipedes, pill bugs, and meal worms. An unsuccessful attempt was made to condition them to eat hamburger or small pieces of beef.

An interesting observation was made by Van Denburgh (1922: 430) regarding the reaction of a colony of ants toward a preying horned lizard.

". . . [*P. m'callii*] was sitting on an ant hill, but not an ant was in sight although a half hour later they were swarming over it. It seemed as though the ants remained under cover in the nest as long as the lizard was watching them." I have several times observed individuals of *P. platyrhinos platyrhinos* on the runways leading to an ant hill that appeared to have normal ant activity including the runway past the lizard. I have placed several of these lizards upon different ant hills in an attempt to observe the phenomenon mentioned by Van Denburgh, but in all instances the lizards left the hills immediately, possibly from fright induced by

being handled. However, Winton (1917:8) observed that these lizards displayed extreme discomfort when stung externally by ants. Little and Keller (1937:216) recorded the death of a horned lizard caged over an ant hill and concluded that the lizard died from being stung by ants.

Movement of the food is necessary before these lizards will show any interest in it. The response toward moving objects seems to be in one of two directions and seems to be controlled by the size of the moving object. If the object is small, the response is one of feeding; if the object is large, the response is an attempt to protect itself or to escape. I have observed this repeatedly with captive horned lizards. Sometimes both responses can be observed in a single group of lizards when the food approaches the maximum edible size.

Feeding upon ants or other small insects is accomplished by an approach which may be from any angle, and a quick flip of the mucous-coated tongue to which the prey adheres. For larger forms the lizard maneuvers so that the attack is made usually on the anterolateral part to the prey; again the sudden flip of the tongue secures the prey, then the head is bent downward with the snout near the ground and this bending is accompanied simultaneously by a sideward movement which often brings the food in contact with the ground. This latter maneuver Bryant (1911:35) has suggested is a means of breaking up large prey. I would rather consider it an aid in the swallowing process which often takes a minute or more in cases involving large insects.

As with most cold-blooded vertebrates, optimum temperature is necessary for active feeding. Norris (1949), in studying the cloacal temperatures of the species *P. m'callii,* found that the extremes for the optimum cloacal temperature were divided by approximately 5°C; presumably the extremes were approximately 36°C and 41°C. Cowles and Bogert (1944), in a temperature study of some of these lizards, supply the following:

	Retreat from cold	active range	Max. voluntary tolerance
P.p.platyrhinos	29 0°C	36 8°C	39 6°C
P.m'callii	29 3°C	36 9°C	41 0°C
P.c.blainvillii	28 0°C	34 9°C	39 0°C

The lizards retreated under the sand at both the upper and lower extremes.

BREEDING HABITS

Both oviparous and ovoviviparous forms occur within this genus. The known oviparous forms include *P. cornutum*, *P. coronatum* (presumably all subspecies), *P. solare*, *P. platyrhinos* (all subspecies), and probably *P. m'callii*. The only species known for certain to be ovoviviparous is *P. douglassii* (presumably all subspecies).

Mating takes place in the spring generally during the months of April, May and June. The exact time is governed to some extent by the general weather conditions and more extensively by the geographic location of the species. Courtship displays and mating behavior have been observed in several cases. Wood (1936:177) presents the courting behavior of a male and female *Sceloporus occidentalis occidentalis* after which he states: "Several horned toads, *Phrynosoma b. blainvillii* (Gray), exhibited a similar behavior. The chief difference here was that the grip on the left side of the neck was firmer and the lizard, raising himself on his fore legs would jerk his head quickly to the right, at the same time pushing forward on all fours, thus turning the female over on her back." His report on *Sceloporus o. occidentalis* is here given:

". . . A large male was pursuing two adult females. He would grasp a female with his jaws, usually by the left side of the neck. Either immediately after grasping the female or after a short pause, he would very actively attempt to push her over on her back. Sometimes she tried to break away and the result was that the two ran about in circles. At other times she made no attempt to escape. Then he would roll her over on her back, all the while firmly retaining his grip on her neck. Sometimes he grasped her by the side of the body and tried to push her over but she would run forward trying to break away. Thus the two would travel about the cage in circles until the male released his hold. . . . Although the author saw this behavior many times, copulation was never observed."

Hewatt (1937:234) observed the behavior of a male and female of the species *P. cornutum*. His observations are as follows:

"Two specimens of *Phrynosoma cornutum* were collected from different localities on April 19, 1936. While they were being held in the writer's hand one of the lizards grasped the other by the loose skin back of the left fore leg and held on tenaciously. When

placed upon the ground the female tried to escape but was held firmly by the male. After the female had subsided, the male grasped her left horn and began to scratch the dorsal region back of the fore legs. Following this irritation the female lizard turned her posterior ventral surface to one side and the male placed his cloacal aperture over that of the female. The female was never on her back but was in a twisted position. With vigorous activity the male everted the copulatory organ and inserted it into the female's cloaca. A close examination revealed that the semen passes along a groove in the copulatory organ. The complete courting and copulation processes occupied sixteen minutes."

Milne (1938:200) observed a pair of copulating *P. cornutum* whose action was, with a few exceptions, mainly as described by Hewatt. The male's position was atop the female upon whom he rode, sometimes with his hind legs dragging on the ground. An interesting account of the "penis" was given by her as follows: "The penis, a very dark red structure covered by a moist mucous membrane, was exposed for fully 13 mm. between the male's cloacal orifice and where the penis curved under the left side of the female's tail to enter her cloacal orifice. The penis after removal (fully distended) measured 31 mm. long by 6 mm. broad by 4 mm. deep, tapering only in the apical third."

The oviparous forms generally lay their eggs shortly after mating. Deposition of the eggs of *P. cornutum* has been observed by Reese (1922), Cahn (1926) and Hewatt (1937). In general, they are all the same. The female excavates a slanting hole in the ground 4 to 6 inches deep and 3 to 4 inches in diameter. Into the hole she deposits her eggs in layers each covered by a small amount of dirt. Two or three layers are deposited depending upon the size of the clutch, which varies from 20 to 40 eggs in *P. cornutum,* 8 to 15 in *P. platyrhinos,* 25 to 28 in *P. solare* and 6 to 14 in *P. c. blainvillii.* The excavation is then completely filled with soil and left without further attention by the adults. Hatching occurs in 40 to 50 days in *P. cornutum* with a slightly longer period in *P. platyrhinos.* In *P. c. blainvillii* the eggs are evidently retained in the oviducts until a few hours before hatching. Bryant (1911:14) reports, "with *P. blainvillii* [*P. coronatum blainvillii*], however, the young hatch a few hours after the eggs are layed . . . , they vary in number from six to fourteen."

In the species *P. douglassii,* which is ovoviviparous, mating takes place in April and May with the young being born in July and August. The number of young is between 8 and 30. Smith, C. F.

(1941:114) records the birth proceedings of a specimen of *P. douglassii hernandesi* as follows:

"Ten of the young were born prior to 9:30 A. M., when the event was first called to the writer's attention. The remaining five arrived at 9:31, 9:42, 9:55, 10:30, 10:45, respectively. Three of the first ten were born between 9:00 and 9:30, but the exact time was not recorded.

"The mother assumed a position with body raised, not touching the ground, dropped the young, and moved off a few inches. She showed absolutely no interest in subsequent events. Birth was accompanied by the discharge of one or two drops of watery fluid.

"Each of the young was surrounded by a watery fluid that was enclosed in a thin, fragile, transparent membrane. In some cases the posterior end of the fetus emerged first, while in others, the opposite end emerged first, but the fetus was always dorsal side uppermost. The fetus was not curled within the membrane except that the tail was pressed tightly against the right side of the body.

"After birth, the fetus remained motionless for a period of time varying in these specimens from five to fifty-five minutes. The first motion was a wriggling one, and was continued, in some cases intermittently, until the egg membrane was broken. Then the lizard gasped for breath, swallowed a few times, and crawled off several steps to dry."

Upon the deposition of the eggs or the completion of parturition, the female's duty is finished and genenrally she shows no interest in the young. However, Lockwood (1883:682) reported observing a *P. cornutum* (probably *P. douglassii brevirostre*) from South Platte Canyon that appeared to show maternal "anxiety" for her young by keeping herself between them and the observer while directing the young into a small depression. Following this she ran across the path of the observer, which he interpreted as an attempt to attract attention away from the, then concealed, young. This is the only known case where this action of these lizards has been interpreted as parental care of the young.

DEFENSIVE HABITS

The rough horny appearance of these lizards would seem to be enough warning to would-be predators without additional defensive displays and mechanisms. A few snakes, however, seem to disregard both appearance and displays only to find themselves victims instead of victors. Cope (1900:404) reports finding a dead snake with the occipital horns of a specimen of *P. cornutum* pro-

truding from the sides of the neck. Vorhies (1948:303) writes that:

"Some 15 years ago there was brought to me a recently born *C. atrox* that had attempted to swallow a horned lizard, *Phrynosoma solare*. It engulfed the head of the lizard, but the horns of the prey penetrated the wall of the neck region of the rattlesnake, so that both predator and prey were locked together and perished in that position."

Bryant (1911:15) lists the rattlesnake *Crotalus* and the roadrunner *Geococcyx californicus* as the two natural enemies of the horned lizard. Miller (1948:67) adds also the prairie falcon *Falco mexicanus* as a possible predator. He presents the following:

"During a lifetime acquaintance with the horned lizards in California, I have never until the past year observed a case of one having fallen victim to a predator. On May 8, 1946, I prepared a freshly taken specimen of the prairie falcon (*Falco mexicanus*) from the desert 30 miles east of Indio, California. In its stomach were the hind feet and the terminal half of the tail of a horned lizard neatly snipped off. In addition there were small fragments of reptile bone that I could not identify with certainty, but have no reason to doubt belonged to the same individual. Mr. Gerhard Bakker, of Los Angeles City College, determined the species as *Phrynosoma platyrhinos* which is the form one would expect from that area."

The rough irregular appearance, of these lizards, and their ability to adapt the basic body colors to fit those of the substrata, permits these lizards to escape the notice of many observers. Their adaptation for burrowing and remaining beneath the sand probably has helped many to escape or be passed by unnoticed.

In several instances they have been observed to defend themselves actively against the advances of a supposed enemy. Cope (1900:411) includes in his discussion of the species *P. douglassii* the following observations made by Dr. Elliott Coues:

". . ., a certain slight means of defense which the 'horns' may sometimes afford is shown by the use they are put to when the animal is irritated by poking with a finger or bit of a stick; then the head is lowered, the horns set forward, the back arched up, and the whole attitude becomes ludicrously like that of a bull in miniature. The horned lizards show special aversion to dogs. On approach of one they raise themselves to the full length of the legs, puff out the body, open the mouth, and hiss audibly, altogether presenting quite a formidable front."

Ditmars (1936:67) described the action of the rare *P. ditmarsi* as follows:

"When annoyed it would arch its back, point its snout downward, then make jumps of fully an inch from the ground, each jump accompanied by a miniature hiss which sounded like a sneeze."

Such displays are not uncommon to those familiar with these lizards. During the winter of 1949-50, captive specimens of both *P. cornutum* and *P. douglassii ornatissimum* were induced to display repeatedly by tormenting them with a moving object such as a finger or a pencil.

The well-publicized blood-squirting from the eyes of certain of these lizards is generally interpreted as a defensive mechanism. Just how the phenomenon repels the enemy is not known. Tests of the blood have failed to show the presence of toxic substances, however, dogs seem to show a great aversion to the lizards after the blood has been released. The blood squirting was first thought to be associated with ecdysis, but repeated reports of ejections by lizards in all stages of the molting cycle seem to disprove this. A histological study and analysis of the tissues following the squirting is presented by Bruner (1907) and Burleson (1942). Discrepancies in the two reports indicate that the process is not as yet well understood.

EVALUATION OF TAXONOMIC CHARACTERS

Since the criteria for speciation in the genus *Phrynosoma* are based primarily upon morphological differences and secondarily upon coloration, it seems wise to define and evaluate the characters most commonly used in the descriptions and diagnoses of these lizards before discussing the origins and relationships of the species. The names used by the earlier workers for any given character, varied, and may lead to erroneous conclusions by subsequent workers.

The distinguishing characters can be divided into three general groupings of: squamation, body proportions, and color and color pattern, under which they will be briefly discussed.

SQUAMATION

Occipital spines: These spines are on the posterior mesial border of the skull. Normally there are two spines present and often there is a short interoccipital spine between them. These spines are reduced in some forms and are entirely missing in *P. ditmarsi.* On the other hand there are four, long, closely set occipital spines in

P. solare. The characters of the occipital spines are of value in the general specific diagnosis as indicated above and likewise in determining the subspeciation in *P. douglassii* and *P. orbiculare* where the proportionate length of the occipital spines to the temporal spines serve as the chief diagnostic characteristic.

Temporal spines: Projecting from the laterally expanded temporal area of the skull, there are normally three pair of temporal spines. However, the range within the genus from complete absence in *P. ditmarsi* to five pairs in *P. platyrhinos* and *P. coronatum.* The spines are of particular importance in distinguishing the subspecies of the species *P. orbiculare, P. douglassii, P. platyrhinos* and *P. coronatum.*

Frontal scales: Unlike many of the lizards that have large, regular, platelike scales on the frontal area of the head, *Phrynosoma* has reduced, irregularly-shaped scales. The texture, size and coloration of these scales are of taxonomic significance, especially in the subspecies of *P. coronatum.*

Superciliary ridge and spine: Extending longitudinally above the eye, and forming the lateral border of the frontal area, the superciliary ridge terminates posteriorly in a superciliary spine. The ridge itself is of little use as a diagnostic character. The size and shape of the spine is distinctive in *P. asio,* but is of little use elsewhere in the genus because of its variability. Attempts to use it in a comparative manner with the postlabials, occipitals or temporals proved unprofitable.

Supralabials and infralabials: The labial series, exclusive of the sublabials, is nearly uniform in both number and character throughout the genus with approximately the same variations occurring in all forms.

Sublabials: The sublabial scales are the small scales separating the infralabials from the chinshields. Depending on the species, arrangement varies from one in which the infralabials and chinshields are in contact, with no sublabials present, to a condition in which they are separated by six or seven rows of sublabials. They are of use in indicating likenesses and differences between the species and provide a useful means for differentiating *P. ditmarsi.* The number of sublabial rows present is directly correlated with the depth of the lower jaw both of which features are dependent upon the size and erectness of the quadrate bone.

Chinshields: The chinshields are on the ventrolateral edge of

the mandible and are of particular importance in the diagnoses of the subspecies of *P. coronatum*.

Postrictal scale: Present in only part of the species, the postrictal scale is a long conical scale at the anteroventral corner of the auricular opening. It is present in some subspecies of *P. coronatum* and absent in others.

Subrictal scale: Also limited to certain species, the flattened subrictal is found between the last chinshield and the postrical scale. Its position is of importance in the diagnoses of the subspecies of *P. coronatum*.

Gular scales: The scales on the throat between the rows of chinshields, from the tip of the jaw posteriorly to the transverse gular fold are collectively called the gular scales. They may be subequal throughout, or there may be one longitudinal row or more of enlarged scales on each side. Three or more enlarged rows are characteristic of *P. asio* and *P. coronatum*. The gular scales are characteristically mildly keeled in *P. boucardii*.

Tympanum: Defined as the membrane across the ear opening, the tympanum in some forms has a tendency to be covered by scales. This is consistently true in only one species (*P. m'callii*) although it occurs in certain populations of other species. Not to be confused with the above covering is the lateral fold of skin, which in some horned lizards conceals the entire auricular opening. The covering by folds of skin is itself a character in several of the groups.

Dorsal body scales: The dorsal scales covering the back from the neck to the base of the tail between the lateral abdominal fringes vary considerably in size and texture on a single specimen of the horned lizards. The general basic covering is of small imbricate scales, among which are several sizes of larger scales; the largest generally form a series of longitudinal rows down the back. The abundance and size of the enlarged scales determines the apparent roughness that is used in a general grouping of the species and in several cases as a minor specific character.

Lateral abdominal spines: One or two lateral abdominal series of soft spines is found in all but one of the species of *Phrynosoma*. The number of lateral series serves to group the species. However, I do not regard such groupings as having a great degree of phylogenetic significance.

Ventral scales: The most significant diagnostic character occurring in the ventral scales is the presence or absence of keeling. The number of transverse or longitudinal rows has been recorded in a

few cases. I have concluded that, owing to the great variation in a single form, the number of rows does not serve as a distinguishing feature.

BODY PROPORTIONS

Head: The proportions of the head vary markedly in the genus. The length of the head measured from the notch between the occipital spines (from base of the interoccipital spine, if present) may be longer than, equal to, or less than the width of the head measured at the angle of the jaw. The ratio of the two measurements has been applied particularly in the diagnosis of the subspecies of *P. coronatum* as well as generally throughout the genus. The degree of bluntness or prolongation of the nose as reflected by the rostro-frontal angle is of use in grouping the species in a general way. Of limited use also are the ratios of such measurements as: eye-snout to head length; ear-snout to head length; frontal-width to head width and the occipital spine length to head length. The general contour of the head and frontal area however, are diagnostic in several species (*P. taurus, P. asio* and *P. douglassii*).

Body proportions: The general proportions of the body are quite similar throughout the genus. Width to length ratios were found to be diagnostic of sex but of little consequence in defining species.

Appendage proportions: Ratios of arm length to leg length or the ratio or either to the total length were found to reflect age and sex differences but to be of little or no use in differentiating subspecies or species. On the other hand, the ratios of the tail length to the total length, to the snout-vent length or to the head length, while also varying with age and sex, was found to be diagnostic of several short-tailed species and subspecies, (*P. braconnieri, P. taurus* and *P. douglassii brachycercum*).

Nostril position: The opening of the nostril with relation to the canthal line will divide the genus into several groups that are otherwise not necessarily closely related. The character is used in the key to help in differentiating several forms.

Femoral pores: The femoral pores are arranged in a row along the ventral surface of the thigh. The pores are generally more conspicuous in the males than the females. This is especially true during the breeding season when the pores of the male are functioning. The number of pores in the row, the location of the pore, whether in a single scale or surrounded by several scales, the number of preanal scales separating the rows and the single versus double row mesially, are significant in many forms. The double row is the only one used as a major character; it characterizes

P. orbiculare. However, the number of scales in each row and the number of preanal scales separating the row are usable as minor characters.

COLOR AND COLOR PATTERN

Head color and color pattern: The basic ground color of the head is generally the same as the ground color or the dorsal area of the body with markings on certain areas forming the color pattern. Color patterns of the head have been used in differentiating the subspecies of *P. coronatum* and also those of *P. douglassii.*

Dorsal color of body and color pattern: These lizards are able to change their color to correspond to that of the substratum upon which they live; thus color alone is an unstable character for differentiating one kind of horned lizard from another. However, the color pattern is generally quite constant and is of importance as a diagnostic character. Color pattern has not been greatly stressed in this study, except in the species *P. douglassii.* Elsewhere other characters were considered to be more reliable and were more easily used.

OSTEOLOGICAL CHARACTERS

In the past, osteological material in this genus has been used, to my knowledge, only on two occasions to provide characters of taxonomic worth. Cope (1900) described the skeletons of *P. douglassii, P. cornutum* and *P. coronatum;* and Bryant (1911) described and compared some of the skeletal elements of the California species. I have had available in this study, skeletons of eight of the fourteen species. In the main, most have been represented by a single specimen. Consequently I have hesitated to use each of several observable differences. Nevertheless, several features seem to be of specific rank. The size, position and erectness of the quadrate bone previously mentioned varies considerably; probably it is largest and most erect in the skull of *P. ditmarsi.* It is slightly smaller in *P. douglassii* and is progressively shorter and more horizontal in *P. cornutum, P. coronatum, P. platyrhinos* and *P. m'callii.* The bone is shortest in *P. solare* where it lies completely horizontal, paralleling the longitudinal axis of the skull. The size and shape of the temporal fossa (figs. 1-8) varies considerably; it seems to be completely closed in *P. m'callii.* The number of teeth on the premaxillary (table 1) as well as the total number of teeth on both the upper and lower jaws seems to be significant in showing relationships. Other characters will undoubtedly prove valuable when a more thorough study of them can be made upon a series of specimens.

SPECIES GROUPINGS

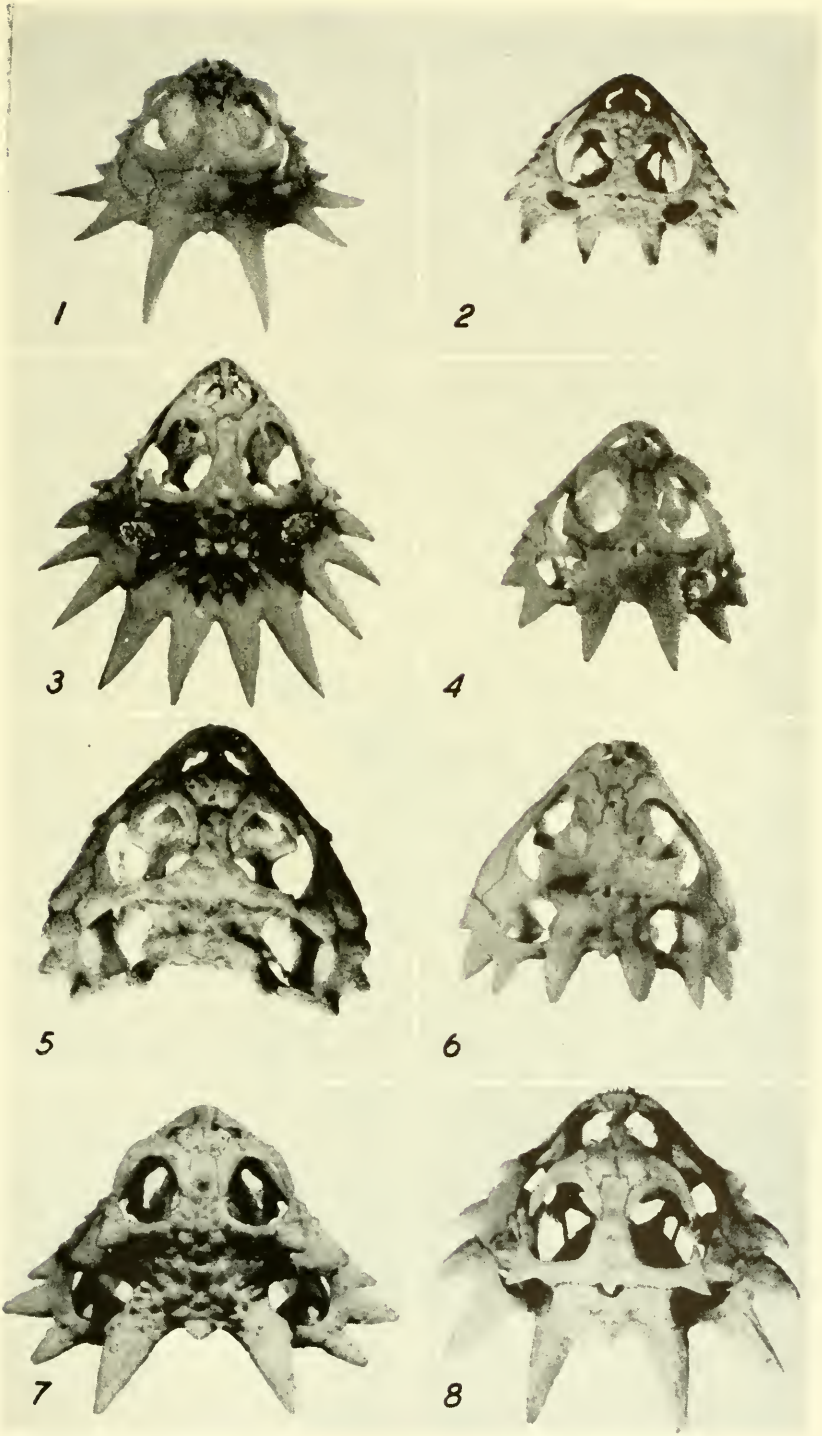
Based upon morphological characters, the genus *Phrynosoma* is found to contain fourteen species, four of which are broken into seventeen subspecies. The fourteen species fall naturally into eight groups of which the *orbiculare* group containing eleven forms, four species and nine subspecies, is the largest. The species and subspecies are as follows:

SPECIES GROUPS

Group	Species	Subspecies
braconnieri	*braconnieri*	
platyrhinos	*platyrhinos*	*platyrhinos*
		calidiarum
		goodei
	m'callii	
	modestum	
coronatum	*coronatum*	*blainvillii*
		coronatum
		frontale
		jamesi
		schmidti
	cerroense	
asio	*asio*	
cornutum	*cornutum*	
solare	*solare*	
taurus	*taurus*	
orbiculare	*douglassii*	*brevirostre*
		brachycercum
		douglassii
		hernandesi
		ornatissimum
		ornatum
	orbiculare	*cortezii*
		dugesii
		orbiculare
	ditmarsi	
	boucardii	

FIGURES 1 to 8. Dorsal views of skulls of eight forms of horned lizards to show variation in the general skull structure. Magnification approximately × 1½.

1. *Phrynosoma m'callii*, KU 21931, Yuma, Yuma Co., Arizona.
2. *Phrynosoma modestum*, KU 473, Magdalina, Socorro Co., New Mexico.
3. *Phrynosoma solare*, EHT-HMS 10441, Santa Ana, N of Guaymas, Sonora, Mexico.
4. *Phrynosoma platyrhinos*, KU 22237, 1-15 mi. S Houserock, Coconino Co., Arizona.
5. *Phrynosoma douglassii ornatissimum*, KU 13943, 3 mi. SW Santa Fe, Santa Fe Co., New Mexico.
6. *Phrynosoma orbiculare cortezii*, KU 25858, Las Vigas, Veracruz, Mexico.
7. *Phrynosoma cornutum*, KU 19544, Devils River Auto Camp, Val Verde Co., Texas.
8. *Phrynosoma coronatum blainvillii*, KU 2730, Los Angeles, Los Angeles Co., California.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7
8

Certain characters common to both the asio and coronatum groups would seem to indicate relationship close enough that they might be included in the same group. However, the distribution of the species involved is such that they appear not to be closely related unless there was a connection between the distal end of Baja California and the mainland of Mexico. Such a connection seems to have little basis geologically or otherwise. The similarities in animals from the two places must, therefore, be considered as independent developments.

PHYLOGENY

In searching for an ancestral form for the genus *Phrynosoma*, paleontology is of little help. Two fossil records are available at this time. One from the late Pleistocene of Arkansas that, according to Gilmore (1928), is indistinguishable from the living forms, and a second from the middle Oligocene of Colorado that has been suggested by Gilmore (1928 & 1941) and Smith (1946) as a possible ancestral form. The latter was described by Cope (1873) as *Exostinus serratus*.

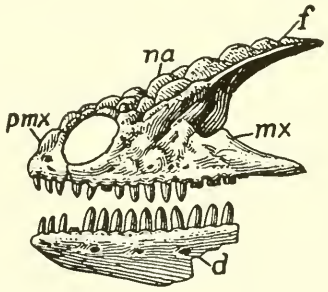

FIG. 1. *Exostinus serratus* Cope, USNM 16565; d, dentary; f, prefrontal; mx, maxillary; na, nasal, pmx, premaxillary. About three and one-half times natural size. (Reproduced from Gilmore, Proc. U. S. Nat. Mus., vol. 91, 1941, p. 75, fig. 32.

From the figure in Gilmore (1941) (reproduced here in figure 1), *Exostinus* would appear to be a lizard somewhat larger than *asio*, the largest living species of *Phrynosoma*. The tubercles of the frontals, nasals, maxillaries and dentaries would certainly seem

comparable with those of *Phrynosoma,* as would the structure and number of teeth. The crucial characteristics of the occipital region of the skull, unfortunately, are not known in the fossil genus.

Based upon the characters of the various living forms, I think that the common ancestral form was of medium to large size, dorsoventrally flattened, bearing medium to small-sized head spines of which there were probably two major occipital and five temporal

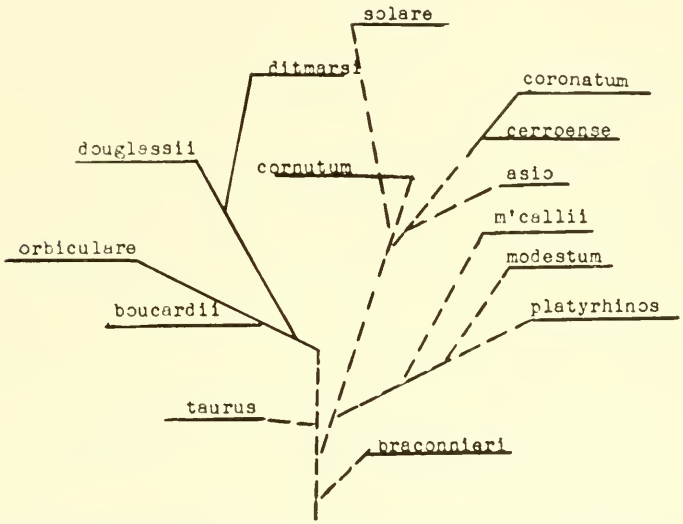

FIG. 2. Phylogenetic tree of the species of *Phrynosoma.* Broken lines indicate probable relationship, solid lines indicate reasonably sure relationship.

spines. The dorsal scales were unequal, the largest being of medium size and not excessively numerous. The tail was of medium length, possibly one half of the snout-vent length. The ventral scales were possibly smooth.

The following figure (fig. 2) expresses the probable relationships of the species in the genus:

SPECIATION

Primitive forms: I regard the species *braconnieri, taurus* and *platyrhinos* as the oldest members in the genus. The first two are monotypic; the latter has three subspecies of which *platyrhinos* shows the most primitive characters.

The most actively differentiating species are found in the or-

biculare, coronatum and platyrhinos groups. Of these, the orbiculare group contains eleven forms—four species, two monotypic —that are contiguous over a large area and I consider it to be the most recently evolved group. Both the coronatum group and the platyrhinos group are thought to have had a secondary dispersal.

Origin: The region consisting of the southern portions of New Mexico, and Arizona, southeastern California and adjoining parts of northern Mexico, probably was the center of origin of the genus. This is supported faunistically by the occurrence of *P. ditmarsi* and *P. solare*, the two most specialized forms, in this region while *P. taurus* and *P. braconnieri*, showing many primitive characters, occur at the periphery of the region occupied by the genus. The platyrhinos group has secondarily invaded the original area as will be seen below. Additional support for such a tenent is forthcoming from geologists which report saline deposits in the area as old as the Miocene epoch. This would seem to indicate the existence of arid conditions which were undoubtedly necessary in the evolution of the genus.

Distribution: The dispersal from the center of origin appears to be divisible into three general movements or waves. The first general movement involved the taurus and braconnieri groups that spread southward deep into Mexico, and the platyrhinos group of which *P. m'callii* moved slightly to the west; *P. modestum* spread to the east and northeast and *P. platyrhinos* spread to the north. A secondary movement of the species *P. platyrhinos* has occurred more recently; it moved southward and reinvaded the original center of dispersal. The second wave dispersed the solare, the cornutum, the asio and the coronatum groups. The solare group remained in the central area, the cornutum group moved east and northeast, the asio group moved south, and the coronatum group moved west. The latter group has more recently differentiated into several forms as it moved into Baja California. The third wave involved only the orbiculare group of which the species *P. orbiculare* and *P. boucardii* have dispersed to the south; *P. douglassii* moved mainly to the north and *P. ditmarsi* remained in the area of the original center of dispersal. The lateness, that is to say recency of the latter wave is indicated by the continuity of the group involved as a whole and by the relatively slight differentiation of the species and subspecies from one another.

Biotic Provinces

The adaptation of horned lizards to a more or less restricted semiarid terrestrial habitat, the small number of species, and the scarcity of specimens of some named forms render these lizards less useful than they otherwise would be as indicators of biotic provinces. Nevertheless, there is a close correlation between the boundaries of species and subspecies of the horned lizards of Mexico and the boundaries of the biotic provinces of that country as drawn by Smith (1939 & 1940). The species and subspecies that are within a single province in the Nearctic Region of Mexico are: *P. braconnieri* (Oaxacan Highland), *P. taurus* (Upper Balsan), *P. m'callii* (Arizonian), *P. platyrhinos goodei* (Arizonian), *P. orbiculare cortezii* (Hidalgan) and *P. coronatum coronatum* (Cape). The distribution of *P. douglassii hernandesi* in Mexico follows, in general, the combined provinces of the Apachian and Durangan provinces extending only slightly into the Chihuahuan. The subspecies *P. orbiculare orbiculare* is confined to the combined area of the Chihuahuan and Tamaulipan provinces. Farther west, *solare* occupies parts of the Apachian, Arizonian and extends slightly into the Sinaloan province.

Two representatives of the genus are found to occur in the Neotropical Region of Mexico. The species *P. asio* ranges from Michoacán on the north to Guatemala on the south, including or transecting the Lower Balsan, the Guerreran (Nearctic), the Oaxacan, Tehuantepecan, Tapachulan and possibly the Chiapan Plateau provinces. The second form, *P. orbiculare dugesii,* is found only in the Lower Balsan Province.

In the United States the geographic ranges of the several species of horned lizards do not coincide with the provinces proposed by Dice (1943). The known distribution of almost any given horned lizard extended over all, or parts, of two or more of Dice's provinces. In only one instance was there a boundary common both to a province and to the range of a horned lizard; that was the line dividing the subspecies *P. p. platyrhinos* from *P. p. calidiarum.*

In analyzing the distribution of the horned lizards of Baja California, their distribution seems to fit best the "Differentiation centers" described by Grinnell (1928). The subspecies with their corresponding "centers" are *P. c. blainvillii* (San Diegan), *P. c. schmidti* (San Pedro Mártir and San Benito Island), *P. c. jamesi* (San Ignacio), *P. c. coronatum* (Cape) and *P. cerroense* (Cedros Island).

TYPE SPECIMENS

The importance of type specimens in taxonomy is well known to those interested in this field. It is to these specimens that we must return to supply the inadequacies of the type description. In many instances types were not designated by the author of the name, thus requiring subsequent workers to attempt, usually by a process of elimination, to determine the specimen or specimens used for the type description. This has been the case in several forms of the genus *Phrynosoma.*

Following are the type specimens that I have examined in this study:

Phrynosoma asio (Cope), United States National Museum No. 32216.

Phrynosoma cerroense Stejneger, United States National Museum No. 11977.

Phrynosoma coronatum frontale Van Denburgh, Stanford No. 93.

Phrynosoma jamesi Schmidt, American Museum of Natural History No. 20583 (paratype only).

Phrynosoma ditmarsi Stejneger, United States National Museum No. 36022.

Phrynosoma douglassii brachycercum Smith, United States National Museum No. 23993.

Phrynosoma douglassii brevirostre (Girard), United States National Museum No. 208.

Phrynosoma douglassii hernandesi (Girard), United States National Museum No. 198.

Phrynosoma douglassii ornatissimum (Girard), United States National Museum No. 204.

Phrynosoma douglassii pygmae Yarrow, United States National Museum No. 11473.

Phrynosoma modestum Girard, United States National Museum Nos. 163 & 164 (nine cotypes).

Phrynosoma nelsoni Schmidt, United States National Museum No. 37585.

Phrynosoma platyrhinos goodei Stejneger, United States National Museum No. 8567a.

Phrynosoma platyrhinos platyrhinos Girard, United States National Museum Nos. 189 (three cotypes).

Phrynosoma platyrhinos calidiarum (Cope), United States National Museum No. 8444.

Phrynosoma regale Girard, United States National Museum No. 161.

Type specimens of the following species and subspecies were not examined in this study:

Phrynosoma boucardii Aug. Duméril & Bocourt, Museum d'Histoire Naturelle, Paris (two males and two females).

Phrynosoma braconnieri Aug. Duméril & Bocourt, Museum d'Histoire Naturelle, Paris.

Phrynosoma brevicornis Boulenger, British Museum of Natural History, London (two cotypes).

Phrynosoma bufonium Wiegmann, Zoologischen Museum, Berlin.

Phrynosoma cornutum (Harlan), type unknown.

Phrynosoma coronatum blainvillii Gray, British Museum of Natural History, London.

Phrynosoma coronatum coronatum (Blainville), Museum d'Histoire Naturelle, Paris.

Phrynosoma douglassii douglassii (Bell), British Museum of Natural History, London.

Phrynosoma douglassii ornatum Girard, type unknown.

Phrynosoma dugesii Aug. Duméril & Bocourt, Museum d'Histoire Naturelle, Paris. (Two cotypes.)

Phrynosoma harlanii Wiegmann, substitute name for *Agama cornuta* Harlan.

Phrynosoma m'callii (Hallowell), Academy of Natural Science, Philadelphia.

Phrynosoma ochoterenai Cuesta Terron, Type was formerly in Museo National, México, now missing.

Phrynosoma orbiculare cortezii (Aug. Duméril & Bocourt), Museum d'Histoire Naturelle, Paris.

Phrynosoma orbiculare orbiculare (Linnaeus), type is presumably an unnumbered figure in Hernandez Plantas Animales de Nueva España . . . , 1615, p. 327.

Phrynosoma planiceps Hallowell, type unknown.

Phrynosoma solare Gray, British Museum of Natural History, London.

Phrynosoma spinimentum Peters, Zoologischen Museum, Berlin.

Phrynosoma taurus Dugès, Museum d'Histoire Naturelle, Paris, (two cotypes).

Phrynosoma Wiegmanni Gray, British Museum of Natural History, London.

Tapaya orbicularis longicaudatus Dugès, Alfredo Dugès Museum, Guanajuato, Mexico.

KEY TO THE SPECIES AND SUBSPECIES OF PHRYNOSOMA

1. Four large occipital spines on posterior periphery of the head continuous with the temporal spines to form a continuous crown. Southern Arizona and Northern Sonora ..... *solare*
1′ Two occipital spines or occipital spines absent or reduced and not continuous with the temporal spines 2
2. Occipital and temporal spines absent; replaced by low rounded protuberances; lower jaw greatly expanded vertically; five or six small sublabials separating chinshields and infralabials ..... *ditmarsi*
2′ Two occipital spines present; lower jaw less expanded; sublabials five or less 3
3. Ventral abdominal scales keeled 4
3′ Ventral abdominal scales smooth 7
4. Temporal area prolonged, terminating in a large spine three or more times the length of the occipital spines ..... *taurus*
4′ Temporal area not prolonged, less than three times the length of the occipital spines; temporal spines same size as, or smaller than occipitals 5
5. Tail reduced (usually shorter than head); Puebla and Oaxaca, Mexico ..... *braconnieri*
5′ Tail not reduced (usually two to three times the length of the head) 6
6. Superciliary spines well developed, equaling, or nearly equaling, the occipital spines; ventral abdominal scales large, 30-40 across widest part of belly; three or four rows of enlarged scales on each side of gular area; one row enlarged soft spines in lateral abdominal fringe. Colima to Guatemala ..... *asio*
6′ Superciliary spines reduced, smaller than occipital spines; ventral abdominal scales small, 50-60 across widest part of belly; one row of enlarged gular scales on each side; two rows of soft spines in lateral abdominal fringe. Kansas, south and southwest through Oklahoma, Texas, New Mexico and northeastern Mexico ..... *cornutum*
7. Three or more rows of enlarged scales on each side of gular area; chinshields serrate and visible from above ..... coronatum group 8
7′ One or no row of enlarged scales, on each side of gular area, chinshields not serrate, not visible from above or if visible only the most posterior ones showing 13
8. Frontal scales large, flat, platelike, dark brown or black with distinct light narrow spaces between them; postrictal scales small or absent; subrictal scales usually in line with chinshields but sometimes slightly above 9
8′ Frontal scales small, convex, rugose (or if large convex and smooth and color the same as remaining portion of head); postrictal scale large; subrictal scale always distinctly above row of chinshields 11
9. Postrictal scale absent or small; subrictal in direct line with chinshields. Cape area of Baja California ..... *coronatum coronatum*

9′ Postrictal scale present and large; subrictal in line or slightly above row of chinshields 10
10. Chinshields four on each side; subrictal in line with chinshields; four temporal spines on each side. Cedros Island ..... *cerroense*
10′ Chinshields five on each side; subrictal slightly above row of chinshields; five temporal spines on each side. Between lat. 26°20′ and 28°40′ Baja California ..... *coronatum jamesi*
11. Frontal scales large, convex, smooth. Southern California and the northwestern part of Baja California ..... *coronatum blainvillii*
11′ Frontal scales small, convex, rugose 12
12. Head as wide as long or slightly wider than long; temporal spines curving posteriorly. Central to southern California, *coronatum frontale*
12′ Head slightly longer than wide; temporal spines projecting laterally, appearing serrate. Between lat. 28°50′ to near 31°50′ Baja California ..... *coronatum schmidti*
13. Length of occipital spines three or four times their basal diameter, 14
13′ Length of occipital spines less than two and one-half times their basal diameter 17
14. Two rows of soft spines in lateral abdominal fringe; tail markedly flattened; dark middorsal streak; ventral abdominal scales immaculate white. Southeastern California, southwestern Arizona and northeastern Baja California ..... *m'callii*
14′ One row of soft spines in lateral abdominal fringe; tail rounded or only slightly flattened; dark mid-dorsal streak absent; dark flecks usually present on the ventral abdominal scales 15
15. Three long temporal spines; occipital spines tend to curve laterally; usually only the last three chinshields greatly enlarged. Southern Arizona and northwestern Sonora ..... *platyrhinos goodei*
15′ Five medium sized temporal spines; occipital spines usually straight; chinshields enlarging gradually from first to last 16
16. Occipital spines long (48-60% of length of head) and broad, giving them a heavy appearance; tail often slightly flattened posteriorly. Southern Utah, Arizona, southern Nevada, California into northeastern Baja California ..... *platyrhinos calidiarum*
16′ Occipital spines short (45% or less length of head); tail rounded posteriorly. From Washington to southern Utah and southern Nevada ..... *platyrhinos platyrhinos*
17. No lateral abdominal fringes; gular scales subequal. Southern Texas, New Mexico and northern Mexico ..... *modestum*
17′ One row of soft spines in lateral abdominal fringe; one row of slightly enlarged gular scales usually present on each side 18
18. Head not strongly notched in occipital area; occipital spines one and one-half to two times as long as their basal diameter 19
18′ Head distinctly notched; occipital spines usually less than one and one-half times their basal diameter 22
19. Frontal area of head concave; occipital spines nearly erect; temporal spines nearly horizontal; gular scales faintly keeled. Guanajuato and Hidalgo ..... *boucardii*

19′ Frontal area flat; occipital and temporal spines both horizontal; gular scales smooth 20

20. Temporal spines extending backward farther than occipital spines; femoral pores usually in single series. Veracruz, *orbiculare cortezii*

20′ Temporal spines equal to or shorter than occipital spines; femoral pores in single or double series 21

21. Occipital spines extending posteriorly beyond temporal spines; femoral pores often forming a double series mesially; ventral abdominal scales often covered with a dark reticulate pattern. Plateau of Mexico . . . . . *orbiculare orbiculare*

21′ Occipital spines and temporal spines projecting posteriorly an equal distance; femoral pores 14-14 confined to a single row; ventral abdominal scales not greatly darkened. Colima, *orbiculare dugesii*

22. Length of tail approximately equal to width of head; gular scales convex; chest scales faintly keeled. Durango and south central Chihuahua . . . . . *douglassii brachycercum*

22′ Length of tail considerable more than width of head; gular scales flat or slightly concave; chest scales smooth 23

23. Temporal area convex; lateral profile of temporal spines forming a curved line if projected to near tip of jaw; length of occipital and temporal spines less than their basal diameter, usually projecting vertically. Width of head at angle of jaw greater than across temporal area; temporal area and spines similar in color to remainder of head 24

23′ Temporal area flattened; lateral profile of temporal spines forming a straight line, if projected to angle of jaw; occipital and temporal spines usually as long as, or longer than, their basal diameter, and generally projecting horizontally; width of head at angle of jaw less than at temporal area; temporal area and spines often lighter colored than rest of head 25

24. Dorsal dark spots edged mesially and posteriorly in light cream; nostrils always piercing the snout laterally. New Mexico, southeastern Utah and southwestern Colorado, *douglassii ornatissimum*

24′ Dorsal dark spots edged only posteriorly in cream; nostrils often piercing snout anterolaterally. Western Kansas and Nebraska, eastern Colorado, Wyoming and Montana . *douglassii brevirostre*

25. Size large. Temporal spines one to one and one-half times as long as their basal diameter, usually projecting horizontally. Southern Utah, Arizona and northern Mexico, *douglassii hernandesi*

25′ Size small; temporal spines as long as their basal diameter; often projecting vertically 26

26. Ground color pale, and pattern often only vaguely discernible; central and northern Utah, and northeastern Nevada, *douglassii ornatum*

26′ Ground color generally dark; pattern distinct. Eastern Washington and Oregon, northeastern part of California, Idaho and and northeastern corner of Nevada . . . . *douglassii douglassii*

TAXONOMY

Phrynosoma braconnieri Aug. Duméril and Bocourt

Phrynosoma braconnieri Aug. Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 1, 1870, pl. 12, fig. 7, 7a-g; Bocourt, *idem*, livr. 4, 1874, pp. 233-234; Garman, Bull. Essex. Inst., vol. 16, 1884, p. 19; Boulenger, Catalogue of the Lizards in the British Museum of Natural History, vol. 2, 1885, p. 248; Gadow, Proc. Acad. Nat. Sci. Philadelphia, 1885, p. 147; Cope, Bull. U. S. Nat. Mus., no. 32, 1887, p. 39; Herrick, Terry & Herrick, Bull. Sci. Lab. Denison Univ., vol. 11, 1899, p. 134; Günther, Biologia Centrali-Americana, Reptilia and Batrachia, 1890, p. 79; Dugès, La Naturaleza, ser. 2, vol. 2, 1896, p. 479; Herrera, Católogo de la Colleción de Reptiles y Batracios, ed. 2, 1904, p. 19; Ditmars, Reptiles of the World, 1910, p. 151; Bryant, Univ. California Publ. Zool., vol. 9, 1911, p. 5; Smith, Trans. Kansas Acad. Sci., vol. 37, 1934, pp. 287, 288, 289, pl. 11, fig. 4; Smith and Laufe, Trans. Kansas Acad. Sci., vol. 48, 1945, p. 338; Smith and Taylor, Bull. U. S. Nat. Mus. no. 199, 1950, p. 100; Univ. Kansas Sci. Bull. vol. 33, pt. 2, 1950, p. 337.

Taxonomic history: This species was named and described by Aug. Duméril and Bocourt (1870) from specimens, in the Museum d'Histoire Naturelle de Paris, collected in Oaxaca by M. Jacob, Alfredo Dugès and A. Boucard. It was placed in the subgenus *Phrynosoma*. Subsequent workers have without exception given full specific rank.

Diagnosis: This small short-tailed species can be diagnosed by the following characters: nostrils within the canthal lines; one row of lateral abdominal spines; ventral scales keeled throughout; temporal spines much reduced; two moderately-developed occipital spines; tail greatly reduced, about one half the width of the head.

Description: Head slightly broader than long; nostrils small, within the canthal lines; internasal distance about three times the diameter of the nasal opening; frontal scales subequal; superciliary spines small; occipital spines short, heavy and divergent; temporal spines reduced to near size of adjoining scales; tympanum exposed; infralabials small, slightly enlarged posteriorly; separated from the small chinshields by a single row of small sublabials; gular scales small, imbricate and subequal; gular fold covered anteriorly with small scales and posteriorly with minute scales; dorsal scales mostly minute; a few enlarged dorsal scales arranged in longitudinal rows; tail short, about one half the head width; single row of lateral abdominal scales originating on the shoulder above the arm and extending to insertion of hind legs; ventral scales keeled throughout; eight or nine femoral pores on each side, separated mesially by about fifteen preanal scales.

Dorsal ground color yellowish gray; two indistinct dark neck spots; several indistinct dorsal body spots, the edges of which fade

into the ground color; a single, narrow, dark, transverse bar on tail; ventral surface yellow with small, dark spots.

Discussion: This rare species is easily recognized by its extremely short tail. Its affinities, although not close, appear to be nearest to the species *P. platyrhinos* and *P. modestum.* The exact measurements of the lizards available for this study are given in Table 2.

Distribution: This species has been reported from the Mexican states of Puebla and Oaxaca. It has been taken from near the border of Veracruz, and may be found to inhabit parts of that State also.

Locality records: MEXICO. *Oaxaca:* no specific locality (5 spec. Mus. d'Hist. Nat. Paris). *Puebla:* Tehuacán (USNM 47386, 11369); 10 mi. NE (EHT-HMS 10445); 22 mi. NE. (EHT-HMS 10444).

Phrynosoma platyrhinos platyrhinos Girard

Phrynosoma platyrhinos Girard, *in* Stansbury's Exploration and Survey of the Valley of the Great Salt Lake of Utah, 1852, pp. 354-363, pl. 7, figs. 1-5; Cope, Proc. Acad. Nat. Sci. Philadelphia, 1866, p. 302; Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale; Études sur les Reptiles, livr. 4, 1870, pp. 232-233; Gentry, Proc. Acad. Nat. Sci. Philadelphia, 1885, p. 147; Stejneger, N. Amer. Fauna, no. 7, 1893, p. 190 (*part.*); Van Denburgh, Occas. Papers California Acad. Sci., no. 5, 1897, p. 98 (*part.*); McLain, Critical Notes on a Collection of Reptiles from the West Coast of North America, 1899, p. 8 (*part.*); Bryant, Univ. California Publ. Zool. vol. 9, 1911, pp. 44-50, pl. 2, figs. 5 and 6, figs. 13-14; Van Denburgh, Proc. California Acad. Sci., ser. 4, vol. 3, 1912, p. 137 (*part.*); Richardson, Proc. U. S. Nat. Mus., vol. 48, 1915, pp. 422-423; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 5, 1915, pp. 100, 105; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 1917, p. 60, (*part.*); Bently, Copeia, 1919, p. 90; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 11, 1921, pp. 40, 43; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, vol. 1, 1922, pp. 421-426, pl. 36, figs. 1-3 (*part.*); Stejneger & Barbour, Check List of the North American Amphibians and Reptiles, 2 ed. 1923, p. 63 (*part.*); Tanner, Copeia, 1927, p. 56; Erwin, Eleventh Biennial Report of the Board of Trustees of the State Historical Society of Idaho, 1928, p. 32; Ruthven, Occas. Papers Mus. Univ. Michigan, no. 243, 1932, p. 3; Stuart, Occas. Papers Mus. Zool. Univ. Michigan, no. 244, 1932, pp. 1-33, pls. 1-2; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed. 1933, p. 69 (*part.*); Burt, Amer. Midl. Nat., vol. 14, 1933, p. 245; Knowlton & Janes, Copeia, 1934, pp. 13-14; Woodbury, Copeia, 1934, p. 52; Brooking, Copeia, 1934, p. 94; Knowlton & Thomas, Copeia, 1936, p. 65; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed. 1939, p. 75, (*part.*); Tanner, Proc. Utah Acad. Sci., vol. 16, 1939, p. 105 (*part.*); Gordon, Oregon State Mono., Studies in Zool., no. 1, 1939, pp. 15, 16, 47, 69; Linsdale, Proc. Amer. Acad. Arts and Sci., vol. 77, 1940, pp. 232-235, map (*part.*); Tanner, Great Basin Naturalist, vol. 1, 1940, p. 141, (*part.*); Slater, Occas. Papers Dept. Biol. College Puget Sound, no. 14, 1941, pp. 82, 93-94; Anderson & Slater, Occas. Papers Dept. Biol. College Puget Sound, no. 15, 1941, p. 111; Tanner, Great Basin Naturalist, vol. 2, 1941, p. 92; Driver, Name That Animal, 1942, p. 247 (*part.*).

Doliosaurus platyrhinos Girard, United States Exploring Expeditions for the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes USN., vol. 20 Herpetology, 1858, p. 409; Girard, Report of the Explorations and Surveys to ascertain the most Practicable and Economic Rail Road Route to the Pacific Ocean, vol. 5, Report upon the Reptiles of the Route, 1859, p. 18 (*part.*).

Phrynosoma platyrhinum Cope, Bull. U. S. Nat. Mus., no. 1, 1875, p. 49; Yarrow, Report of the Geography and Geology of the Surveys West of the 100th Meridian, under Lt. Wheeler, vol. 5, Zoology, 1875, p. 578 (*part.*); Coues, *idem*, 1875, p. 594 (*part.*); Yarrow & Henshaw, Annual Report of the Chief of Engineers for 1878 of the Surveys West of the 100th Meridian, app. NN, 1878, p. 224, (*part.*); Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, pp. 11, 65 (*part.*); Ditmars, The Reptile Book, 1907, p. 158 (*part.*).

Phrynosoma platyrhinum Boulenger, Catalogue of Lizards in the British Museum of Natural History, vol. 2, 1885, p. 247 (*part.*).

Anota platyrhina Cope, Rept. U. S. Nat. Mus. for 1898, (1900), pp. 443-447, fig. 81 (*part.*).

Phrynosoma platyrhinos platyrhinos Klauber, Copeia, 1935, pp. 178-179; Graf & Jewett, Copeia, 1939, p. 103; Owen, Copeia, 1940, p. 170; Johnson, Copeia, 1942, p. 16; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 19, 1943, p. 95 (*part.*); Evender, Copeia, 1946, p. 257; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, pp. 363, 375 (*part.*); Smith & Taylor, Bull. U. S. Nat. Mus. no. 199, 1950, p. 101 (*part.*).

Taxonomic history: Girard (1852:354) named this species from specimens collected by the Stansbury Expedition to the Great Salt Lake. The latter was given as the known distribution, and remains as the type locality of the form. In the collection at the United States National Museum, three specimens (Cope 1900:466 listed four specimens) all under No. 189 from Salt Lake Valley, Utah, seem to be the specimens used by Girard in his description, and have been designated as the types on the records of that Museum. Other specimens, (No. 190, with three specimens and 191 with five specimens), were also taken by members of the same military company.

Cope (1900) placed *platyrhinos* along with *m'callii* and *calidiarum* in the genus *Anota* based on the concealment of the tympanum by a scaly integument. The character is not constant in *platyrhinos* and *calidiarum;* therefore Cope's arrangement was discarded. Klauber (1935) finding intergrading trends between *platyrhinos* and *goodei*, reduced both to subspecific rank.

Diagnosis: Occipital horns moderately long (usually less than 45 percent of head length); tail round; five to six temporal horns each being slightly longer than the preceding one; interoccipital space approximately equal to basal diameter of spine.

Description: Head slightly longer than broad; frontal area inclined forward, center indented by groove from occipital shelf; rostro-frontal angle acute; nostrils within the canthal line, separated by a distance equal to three times their diameter; superciliary

ridge prominent, composed of four or five enlarged scales; superciliary spine short, broad; posterior limits of frontal area indented; occipital spines moderately long, less than 45 percent of head length, slender; interoccipital space approximately equal to basal diameter of one spine; interoccipital spine small; temporal area moderately expanded; five temporal spines enlarging posteriorly, last approximately one half size and length of occipital; supralabials 10-10, small and serrate; infralabials small, inconspicuous, separated from chinshields by one row of sublabials; chinshields 8-8, increasing in size posteriorly, penultimate largest; gulars subequal except for one row of slightly enlarged scales on each side; two lateral neck patches of enlarged soft spines, lower larger; tympanum exposed; dorsal scales small, smooth, imbricate; enlarged keeled scales few, largest forming a single paired row next to and paralleling vertebral column; two rows of slightly enlarged scales on tail; ventral scales smooth; femoral pores 11-12; rows separated mesially by three preanal scales.

Dorsal ground color light bluish gray; nuchal and body markings brownish black, interspersed with ground color; three irregular transverse bars across back, expanding laterally to form a nearly-solid lateral longitudinal stripe; tail traversed by six dark bands; head olive-gray, with brown to black flecks usually on tips of scales; ventral gular area and abdominal area spotted with black; several larger brown to black spots on preanal area and posterior part of hind limbs.

Variation: Counts of the scales and pores will vary slightly from that given. The length of the occipital spine may approach half the length of the head in a few specimens, especially in those from areas where *P. p. platyrhinos* intergrades with *P. p. calidiarum*. The ground color will vary with the substratum but is generally darker than in the southern subspecies.

Locality records: CALIFORNIA. *Lassen Co.:* Litchfield, 5 mi. E (MVZ 36086); Warm Springs (MVZ 24514-15), 1 mi. S (MVZ 24516) 3 mi. NW (MVZ 24513).

NEVADA. *Churchill Co.:* Fallon (USNM 118606), 5 mi. N (MVZ 20106); Soda Lake, 3 mi. NW (MVZ 28586); *Elko Co.:* Wendover, 3 mi. S (MVZ 12319); *Eureka Co.:* Beowawae (USNM 45290); Emigrant Pass, 3 mi. W (MVZ 18456); Romano, 4 mi. SE (MVZ 20615); Tenabo, 12 mi. NNE (MVZ 20618); *Humboldt Co.:* Golconda, 1 mi. S (MVZ 20611), 5 mi. NE (MVZ 20613), 6 mi. SE (MVZ 30170-73, 30174-79); Golconda (USNM 45289); *Lander*

Co.: Battle Mountain, 14 mi. N (MVZ 20606); Birch Creek Ranch, 6 mi. S (MVZ 12147); Tenabo, 10 mi. NNE (MVZ 20616-17); *Lincoln Co.:* Panaca (USNM 18378-80), 21 mi. W (MVZ 14251-52); Sand Springs (MVZ 14249); no specific locality (USNM 18382-83); *Lyon Co.:* Dayton, 6½ mi. E (MVZ 20110); Fallon, 22 mi. W (MVZ 20107), 27½ mi. W (MVZ 20109); Wabaska, 10 mi. E (MVZ 32096); Wellington, 10 mi. E (MVZ 17117); Yerington, 11 mi. S, 2 mi. E (MVZ 17120); *Mineral Co.:* Huntoon Valley (MVZ 10861); Morgan's Ranch, 2 mi. NW (MVZ 17110); Pine Grove, 6 mi. NE (MVZ 17116); Wichmann (MVZ 36297); *Nye Co.:* Daylight Springs (LMK 22135); Hot Creek, 10 mi. N (MVZ 16222); Millet, 5 mi. S (MVZ 12143, 14366); North Twin River (MVZ 16177); Round Mountain (USNM 52448-49); Toquema Range, Jefferson Creek (USNM 52446); Toyabe Range, Peavine Creek (USNM 52447); Wisconsin Creek (MVZ 12824). *Ormsby Co.:* Carson City (USNM 44814-15). *Pershing Co.:* Fanning, 10 mi. E, 3 mi. S (MVZ 21470); Lovelock, 30 mi. W, 4 mi. N (MVZ 21478); Sulphur, 10 mi. W, 6 mi. N (MVZ 21476); Toulon, 3 mi. NNE (MVZ 18453-54); Vernon, 3 mi. S (MVZ 21472). *Storey Co.:* Virginia City (USNM 8650). *Washoe Co.:* Gerlach, 2½ mi. E, 11 mi. N (MVZ 21483, 21487-88); Little High Rock Canyon (MVZ 7533, 7536-38, 7540-41); Pahrum Peak, 4 mi. W (MVZ 24520); Pyramid Lake, East Shore (LMK 38318-19), (USNM 9515, 44813, 50700-03, 50814-19, 58660), Sutcliff (LMK 27293); Reno (USNM 44817-18, 79355-56), 10 mi. E (MVZ 14927), 25 mi. N (MVZ 25324); Smoke Creek 100 yds. E California line (MVZ 20476); Wadsworth (USNM 44812, 50704). *White Pine Co:* Baker (MVZ 11326, 11329-33), 4 mi. NE (USNM 86955); Hamilton, 3 mi. SW (MVZ 12318); Smith Creek Cave (MVZ 42521), 1 mi. SE (MVZ 24503-31), 3 mi. E (MVZ 24527-29); Smoke Creek Desert (USNM 45285-88).

Idaho. *Ada Co.:* Boise (BYU 8064-65), USNM 63266), 15 mi. S (BYU 8061). *Canyon Co.:* Snake River, near Givens (LMK 1448-49. *Elmore Co.:* Cleft, 4 mi. S (USNM 65192-94); no specific locality (USNM 58616). *Owyhee Co.:* Indian Cave (BYU 8060); Murphy (USNM 48153); no specific locality (USNM 42131). *Payette Co.:* Payette (USNM 45231-32).

Oregon. *Harney Co.:* Alvord Lake (USNM 44673). *Malheur Co.:* White Horse Creek (USNM 53042-43).

Utah. *Beaver Co.:* Cove Fort (BYU 8034); Jackson Hill (USNM 36351). *Box Elder Co.:* Kosmo (LMK 26707); Locomotive Springs

(LMK 26708); Promontory Ridge (LMK 23594); Snowville (LMK 24995-96). *Carbon Co.:* Price (BYU 8029, 8031, 8033). *Juab Co.:* Callio (BYU 8091, 8022-23); Trout Creek (UU 1217-18), (LMK 22995). *Millard Co.:* Delta, 5 mi. N (LMK 897), 20 mi. NW (LMK 660); Gandy (BYU 9021); Fillmore (Ruthven, 1932); Hinckley, 10 mi. W (BYU 8028), 15 mi. S (BYU 4313); Middle Pahvant Valley (Stuart, 1932); Simpson's Ranch, 2 mi. E (Burt, 1933). *Salt Lake Co.:* Salt Lake (USNM 189, 190, 4980). *San Pete Co.:* Indianola (BYU 8032). *Sevier Co.:* Monroe (LMK 39394), 5 mi. SW (LMK 38266), 5 mi. W (LMK 38383-84), 12 mi. W (LMK 37871-73, 37945-50). *Tooele Co.:* Cedar Mts. (UU 202); Delle (UU 937); Gold Hill (BYU 2024, 8030), (UU 2119); Grantsville (UU 2007); Iosepa (LMK 26706), 15 mi. N (BYU 8039-44), 18 mi. N (BYU 8020); Low (UU 936); Orr's Ranch (UU 2233), 8 mi. N (LMK 22994, 26709); Willow Springs (UU 1224a). *Uintah Co.:* Jensen, 25 mi. SE (UU 2637); Ouray, 3 mi. E (UU 345). *Utah Co.:* Cedar Fort (USNM 44761); Fairfield (USNM 8107); Goshen (BYU 8063, 8066); Lehi, 4 mi. W (BYU 2086, 2090, 2781); Provo (BYU 4314); Utah Lake, west of (UU 2210-16, 2023-25, 2069-74). *Weber Co.:* Ogden (UU 1699).

WASHINGTON. *Walla Walla Co.:* Fort Walla Walla (USNM 10832).

Phrynosoma platyrhinos calidiarum (Cope)

Phrynosoma platyrhinos Stejneger, N. Amer. Fauna, no. 7, 1893, p. 190, pl. 2, figs. 4a-c (*part.*); Van Denburgh, Occas. Papers California Acad. Sci., no. 5, 1897 (*part.*); McLain, Critical Notes on a collection of Reptiles from the West Coast of North America, 1899, p. 8 (*part.*); Grinnell & Grinnell, Throop Inst. Bull., no. 35, 1907, p. 57; Bryant, Univ. California Publ. Zool., vol. 9, 1911, pp. 4, 44-50, pls. 2, 6 (*part.*); Van Denburgh, Proc. California Acad. Sci., ser. 4, vol. 3, 1912, p. 157, Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 3, 1913, pp. 393, 406; Atsatt, Univ. California Publ. Zool., vol. 12, 1913, p. 38; Camp, Univ. California Publ. Zool., vol. 17, 1916, p. 527; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 1917, p. 60 (*part.*); Hall & Grinnell, Proc. California Acad. Sci., ser. 4, vol. 9, 1919, p. 48; Nelson, Mem. Nat. Acad. Sci., vol. 16, 1922, p. 114; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 2 ed., 1923, p. 63 (*part.*); Tanner, Copeia, 1927, p. 56 (*part.*); Springer, Copeia, 1928, pp. 101-102; Woodbury, Copeia, 1928, p. 17; Klauber, Bull. Zool. Soc. San Diego, no. 4, 1928, p. 3 and *idem*, no. 5, 1930, p. 4; Bogert, Bull. So. California Acad. Sci., vol. 29, 1930, p. 8; Linsdale, Univ. California Publ. Zool., vol. 38, 1932, p. 349; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed. 1933, p. 69 (*part.*); Klauber, Bull. Zool. Soc. San Diego, no. 11, 1934, p. 12; Gloyd, Bull. Chicago Acad. Sci., vol. 5, 1937, p. 112; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed., 1939, p. 75 (*part.*); Cowles, Science, NS, vol. 90, 1939, pp. 465-466; Tanner, Proc. Utah Acad. Sci., vol. 16, 1939, p. 105, (*part.*); Great Basin Naturalist, vol. 1, 1940, p. 141 (*part.*); Linsdale, Proc. Amer. Acad. Arts.

and Sci., vol. 77, 1940, pp. 232-235, map (*part.*); Driver, Name That Animal, 1942, p. 347 (*part.*); Miller, Copeia 1948, p. 67.

Doliosaurus platyrhinos Baird, Report of the Exploration and Surveys to ascertain the most Practicable and Economic Rail Road Route, to the Pacific Ocean, vol. 5, Report upon the Reptiles of the Route, 1859, p. 18 (*part.*).

Phrynosoma platyrhinum Yarrow, Report of the Geography and Geology of the Surveys West of the 100th Meridian, under Lt. Wheeler, vol. 5, Zoology, 1875, p. 578 (*part.*); Coues, *idem*, 1875, p. 594 (*part.*); Yarrow & Henshaw, Annual report of the Chief of Engineers for 1878, Survey West of the 100th Meridian, Appendix NN, 1878, p. 224, (*part.*); Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, pp. 11, 65 (*part.*); Ditmars, The Reptile Book, 1907, p. 158 (*part.*).

Phrynosoma mccallii Yarrow & Henshaw, Annual Report of the Chief of Engineers for 1878, Survey West of the 100th Meridian, Appendix NN, 1878, p. 225; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 65; Boulenger, Catalogue of Lizards in the British Museum (Natural History), vol. 2, 1885, p. 246.

Phrynosoma platyrhinus Boulenger, Catalogue of Lizards in the British Museum (Natural History), vol. 2, 1885, p. 247 (*part.*); Meeks, Field Columbian Mus. Zool. Ser., vol. 7, 1906, p. 12.

Anota calidiarum Cope, Amer. Nat., vol. 30, 1896, p. 833; Cope, Rept. U. S. Nat. Mus. for 1898, (1900), p. 439, fig. 79.

Anota platyrhina Cope, Rept. U. S. Nat. Mus. for 1898 (1900), p. 443, fig. 81 (*part.*).

Phrynosoma calidiarum Ditmars, The Reptile Book, 1907, p. 157, pls. 46, figs. 10, 14, and 50, fig. 2.

Phrynosoma platyrhinus Stephens, Trans. San Diego Soc. Nat. Hist., vol. 3, p. 62.

Phrynosoma platyrhinos platyrhinos Klauber, Copeia, 1935, pp. 178-179; Cowles & Bogert, Herpetologia, vol. 1, 1936, p. 38; Fitch, Herpetologia, vol. 1, 1939, p. 151, Klauber, Bull. Zool. Soc. San Diego, no. 14, 1939, pp. 94-95; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 95 (*part.*); Lowe, Herpetologia, vol. 4, 1947, p. 77; Smith & Taylor, Bull. U. S. Nat. Mus., no. 199, 1950, p. 101 (*part.*); Univ. Kansas Sci. Bull. vol. 33, pt. 2, 1950, pp. 363, 375 (*part.*).

Taxonomic history: This form was first described as *Anota calidiarum* by Cope (1896:833) from a specimen, in the United States National Museum, taken in Death Valley, California. It was placed in the synonymy of *P. platyrhinos* by subsequent workers.

Diagnosis: Occipital horns heavy and long (45 percent or more of head length); interoccipital space one half basal diameter of occipital spine; five to six temporal spines each longer than the one preceding it; tail often somewhat flattened posteriorly.

Description: Head slightly longer than broad; frontal area inclined forward; rostrofrontal angle abrupt; nostrils within canthal lines, medium size, separated by a distance equal to approximately three times their diameter; superciliary ridge distinct, ending posteriorly in a broad triangular superciliary spine; posterior edge of frontal area notched; shallow groove extending from notch to rostrum; occipital spines long and heavy; interoccipital space equal to approximately one half basal diameter of one occipital spine; small interoccipital; enlarged scale at outer base of occipital; tem-

poral shelf moderately expanded; six temporal spines, increasing in size posteriorly, last spine approximately one half size of occipital; occipitotemporal space equal to basal diameter of occipital spine; supralabials small, serrate, 9-9; infralabials small, inconspicuous; chinshields increasing in size posteriorly, penultimate largest; chinshields and infralabials separated by a single row of sublabials; gular scales subequal, one slightly enlarged row on either side; two lateral neck patches of enlarged scales, upper smallest; tympanum free of scaly integument, hidden by fold of skin; dorsum covered with small, smooth, imbricate scales, with a few moderately enlarged keeled scales scattered over back and tail; one row of enlarged soft spines in lateral fringe; ventral scales smooth throughout; femoral pores 8-8, the rows separated mesially by six preanal scales.

Dorsal ground color light yellowish tan; nuchal blotches light gray to black; three gray to black dorsal blotches forming indistinct transverse bands across back; five wide transverse bars on tail; color of venter ivory throughout.

Variation: The length of the occipital spines varies from 47 percent of the head length to a maximum of 60 percent. Accompanying the increase in length is a more noticeable increase in the diameter of the spine giving it a heavy, stout appearance. Either the sixth, fifth or fourth temporal spine may be absent, in which case the bases of those remaining are in contact with each other maintaining an unbroken contour. Near the center of the geographic range of the subspecies, the largest of the temporal spines is normally one-half as large as an occipital spine, but may be smaller in specimens from the outer part of the range.

The tympanum may be partly exposed or completely concealed by a scaly integument, but usually it is hidden by a fold of skin in the lateral neck region.

The general ground color varies with the substratum upon which the animal lives and usually it is lighter than that of the more northern subspecies, *P. p. platyrhinos.*

Discussion: The extensive distribution and altitudinal range of the form heretofore known as *P. platyrhinos platyrhinos* has caused many workers to wonder whether several forms were not involved. After an extensive study of several hundred specimens from all parts of the range, the only division that seems justifiable is the separation of the form here called *P. p. calidiarum.* Cope described *Anota calidiarum*, from specimens taken in Death Valley, California, which

falls within the range of the revived form. It therefore, seems proper to apply that name to the subspecies here defined.

Locality records: Arizona. *Coconino Co.:* Lee's Ferry (UU 1459), (USNM 44632-33); Pipe Springs (SSNH 12744). *Maricopa Co.:* Forepaugh (LMK 26961); Gila Bend (SSNH 17150), (LMK 35180), 1 mi. S (LMK 37734), 4 mi. N (SSNH 14181-83), 30 mi. E (SSNH 17090); Phoenix (USNM 45115); Piedra (LMK 27126); Sentinel (SSNH 15207); Stanwix (LMK 27125); no specific locality (USNM 61387). *Mohave Co.:* Chemehuevis Mts. Lucky Star Mine (SSNH 17179-80); Hackberry (USNM 60174); Sacramento Valley, south end (SSNH 17183-84); Virgin Valley (USNM 18363-73); Wolf's Hole, 4 mi. N (SSNH 17151-55). *Pima Co.:* Ajo, 3½ mi. S (LMK 39115), 6½ mi. S (LMK 39111), 9½ mi. S (LMK 38516). *Yavapai Co.:* Congress Junction, 4 mi. S (LMK 32377). *Yuma Co.:* Dome, 15 mi. N (LMK 39749); Kofa Mts., Del Oso Pass (SSNH 17976-77); Mohawk (LMK 34926); Mohawk Valley (LMK 23602); Parker Indian Agency (USNM 16804); Stoval, 2 mi. N (SSNH 13919); Tinajas Altas (SSNH 17058), (LMK 27014), (USNM 21726); Tule Tanks (LMK 34925); Yuma Desert (LMK 23601).

California. *Imperial Co.:* Chocolate Mts. (LMK 33941-42); Colorado Desert (USNM 8649); Coyote Well (MVZ 1000), (SSNH 11297, 12078), (LMK 34589), (USNM 21962-63); Mountain Spring (LMK 10938); Niland, 5 mi. S (SSNH 15558); Ocotello (LMK 25528); Painted Gorge (SSNH 13921); Potholes (LMK 2448); Yuha Well (LMK 31234). *Inyo Co.:* Argus Mountains (USNM 18431-34), Junction Ranch (SSNH 16986-87); Caso Mountains, north end (LMK 25367); Death Valley (USNM 18411, 64283); Bennett's Well (USNM 8412); Deep Springs Valley (MVZ 31706-07); Emigrant Canyon, Panamint Mts. (MVZ 6638-39); Funeral Mountains (LMK 2534-37); Furnace Creek Ranch (MVZ 7438, 6630, 6637), (USNM 18413-14); Furnace Wash (MVZ 6343); Independence (USNM 18439-41); Keeler (MVZ 3688); Little Lake (LMK 38325), 2 mi. S (LMK 25368); Lone Pine, 3 mi. W (MVZ 6644); Mountain Springs Canyon (MVZ 35829); Owens Lake (USNM 18429); Owens Valley (USNM 18430); Panamint Range (USNM 18417-21); Panamint Valley (USNM 18523-38, 64277-82); Shoshone, 2 mi. N (MVZ 6641); Telescope Peak, Johnson's Canyon (MVZ 4461); Towne's Pass, 2 mi. N (LMK 25369), 5 mi. N (LMK 25370), 6 mi. N (LMK 25371); Walker Creek (MVZ 38392). *Kern Co.:* Chimney Creek (MVZ 2873-77); China Lake (LMK 22202-03); Johannesburg

(MVZ 26033); Red Rock Canyon (LMK 22136); Randsburg (SSNH 21312); Weldon, 16 mi. SSE (MVZ 2879). *Los Angeles Co.:* Antelope Valley (USNM 54813); Coas (USNM 18435); Llano, 10 mi. E (LMK 29204); Lone Mills (USNM 58662-64); Love Joy Spring (USNM 81081); Palmdale (LMK 33436, 34367); Pearblossom, 4 mi. SE (LMK 37430-31); no specific locality (MVZ 3511). *Mono Co.:* Benton (MVZ 3694), 5 mi. N (SSNH 16273); Benton Sea, 2 mi. S (MVZ 3693). *Riverside Co.:* Blythe, 20 mi. W (LMK 39768); Cottonwood Springs (MVZ 4115-16); Desert Center (LMK 2755, 4310-11, 4341-42, 4512, 4856-57), 14 mi. W (LMK 39767); Garnet (LMK 39771-73), (USNM 75136); Hopkin's Well, 4 mi. W (LMK 39774); Little San Francisco Mts., Berdoo Canyon (LMK 31625, 31627, 33111); Mecca, 60 mi. E (MVZ 7867-70); Palm Springs (USNM 18443, 19096-97, 26375), 8 mi. SE (SSNH 13920); Palm Springs Canyon (LMK 34257); Imperial Valley (USNM 75125). *San Bernardino Co.:* Amboy (LMK 7620), 14 mi. S (LMK 39906); Atolia (SSNH 12319); Barstow (USNM 44616), (MVZ 10748), 3 mi. NE (LMK 35653); Blythe Junction, 4 mi. E (MVZ 5495), 14 mi. NE (MVZ 5496); China Lake (LMK 22134); Cronise, 4 mi. E (LMK 39910); Dagget (LMK 7615); Drinkwater Springs (MVZ 18029); Grommet, half way between & Rose (LMK 37651-57); Hodge (LMK 23373); Ibex Pass, 7 mi. S (LMK 39915); Jim Gray (LMK 31720); Klinefelter (LMK 7621); Lavic (LMK 10643), 7 mi. S (MVZ 7444, 7447); Lucerne (LMK 27327); Ludlow (USNM 45179); Mace (LMK 28932); Mohave Desert (USNM 9195, 8651); Mountain Pass, U. S. Highway 91 (LMK 25527); Needles (MVZ 1103-04, 4255), 15 mi. W (LMK 20989), 25-50 mi. W (LMK 38706-07); Old Woman Spring (LMK 27330); Oro Grande (MVZ 7448); Red Mountain (LMK 28933); Rock Corral, 3 mi. E (LMK 31626); Twenty-nine Palms (LMK 8501), north of (LMK 32988-89), 10 mi. E (LMK 39925, 40022), 13 mi. E (LMK 39923); Two Springs (MVZ 18030); Victorville (USNM 44615); Virginia Dale Mine, 1 mi. S (MVZ 44611-12); Walker Station (LMK 25582); Windmill, 3 mi. N (LMK 27322). *San Diego Co.:* Agua Caliente (SSNH 16543); Benson's Dry Lake (SSNH 16726), (LMK 22849, 23701, 23935-36, 24035, 26960, 27324, 33336); Box Canyon (SSNH 11076); Borego Valley (LMK 22137, 26796, 27401); Coyote Creek (LMK 25304); Hodge (LMK 2538); La Puerta (SSNH 11295, 11298-99, 11405, 11701), (LMK 23372); Narrows (LMK 23934); Palm Springs (SSNH 11497, 11077-87); San Felipe Canyon (SSNH 11296); San Felipe Valley (SSNH 16544); Top of Sentenac Canyon (LMK

29494); Vallecitos (LMK 38101); Yaqui Well (LMK 25889); Yaqui Pass (LMK 33761). *San Luis Obispo Co.:* Shandon, 7 mi. SE (LMK 37539).

Baja California. Seven Wells, Colorado Desert (USNM 21964); Montes de Nedia, E base San Pedro Mártir Mountains near San Felipe (LMK 25252); Pozo San Augustín (USNM 37591); San Felipe, 1 mi. N (LMK 38264), 20 mi. N (LMK 38067-68), 50 mi. N (LMK 38069).

Nevada. *Clark Co.:* Boulder Dam (BYU 8038, 455); Boulder City (USNM 101154); Charleston Park, 12 mi. E (MVZ 20103); Fort Mohave, 1½ mi. NW (MVZ 20099-100); Indian Springs, 1 mi. S (LMK 27701); Jean, 10 mi. S (LMK 25888, 29228); Las Vegas (USNM 18391-92), 8 mi. NW (LMK 29093-94); Mesquite (SSNH 12745); Potosi Mountains, 3 mi. N, 6 mi. W (MVZ 35833), 9 mi. W, 2 mi. N (MVZ 35834); Virgin River Narrows, Meade Lake (BYU 4311-12). *Esmeralda Co.:* Arlemont (MVZ 10604, 10606), 7 mi. N (MVZ 10609, 10612-13, 10617-19, 10623); Cane Springs (MVZ 10825, 10830); Fish Lake (MVZ 10826); Gap Springs (MVZ 10616); Tonopah, 12½-13½ mi. W (LMK 37540-42). *Lincoln Co.:* Carp, 4 mi. NE (MVZ 20101); Crystal Springs (MVZ 14240-41, 14236, 14250), 1½ mi. NE (MVZ 14244); Dead Mountains, Hiko Springs (MVZ 19300); Groom Baldy Mt., 14 mi. NNW (MVZ 14253). *Nye Co.:* Amargosa Desert (USNM 18393-95); Ash Meadow (USNM 18396-406, 64384); Grapevine Mountains (USNM 18381); Grapevine Peak, 6 mi. E, 1 mi. N (MVZ 35830-31); Springdale, west of (MVZ 35832); Stonewall Mountains, west side (MVZ 36079-80).

Utah. *Washington Co.:* Beaver Dam (UU 1955, 1982), mountains (BYU 2735), slope (UU 1941, 1952-54, 1956-57, 1983, 2815); Bloomington (UU 370); Harrisburg (LMK 25583); Hurricane (UU 692); (BYU 3364-65); Mountain Meadow (USNM 18377); St. George (USNM 18374-76, 9403, 44723), (UU 389, 2816), (LMK 23809-10), 3 mi. S (UU 439); Springdale (LMK 24994); Washington, 4 mi. E (LMK 25529); Zion National Park (UU 438).

Phrynosoma platyrhinos goodei Stejneger

Phrynosoma hernadezi Streets, Bull. U. S. Nat. Mus., 1877, no. 7, p. 36.
Phrynosoma goodei Stejneger, N. Amer. Fauna, no. 7, 1893, p. 191, pl. 11, figs. 3a-c; Ditmars, Reptiles of the World, 1910, p. 151; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, vol. 1, 1922, pp. 368, 426-427.
Anota goodei Cope, Ann. Rept. U. S. Nat. Mus. for 1898 (1900), pp. 436, 442, fig. 80.

Phrynosoma platyrhinos goodei Klauber, Copeia 1934, no. 4, pp. 178-179; Smith, Annals Carnegie Mus., vol. 27, 1939, p. 315; Smith & Laufe, Trans. Kansas Acad. Sci., vol. 48, 1945, p. 338; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, p. 344; Bull. U. S. Nat. Mus. no. 199, 1950, p. 102.

Diagnosis: Three enlarged temporal spines, the last equal in size to the occipital spines; last three chinshields greatly enlarged and pointed.

Description: Head equally as broad as long; rostrofrontal angle abrupt (60°-70° angle); frontal area flat, posterior border indented to approximately one half frontal length; superciliary ridges prominent, scales enlarged, terminating posteriorly in slightly enlarged pyramidal scale; nostrils within canthal lines, separated mesially by distance equal to twice diameter of nostril; occipital spines moderately large, separated by distance approximately equal to their basal diameter; small interoccipital present; two enlarged tubercles on frontal shelf in contact with an enlarged scale pierced by pineal foramen; three temporal horns, last largest, somewhat separate from other two, approximately equal to occipitals; two enlarged tubercles anterior to first temporal; tympanum concealed; supralabials and infralabials small and inconspicuous; chinshields 7-7, last three greatly enlarged and pointed; one paired row of slightly enlarged scales on gular; two lateral neck patches of soft spines, the lower larger; back covered with minute scales interspersed with varying sizes of larger keeled scales; largest dorsal scales surrounded by rosette of smaller scales, former arranged in three pairs of indistinct longitudinal rows; tail scalation similar to that of back; enlarged scales fewer and smaller; one row of enlarged soft spines in lateral abdominal fringe; latter extending from shoulder to groin; dorsal humeral scales enlarged and keeled; single row forming fringe on posterior border of forearm; leg with scattered enlarged scales; ventral scales smooth; femoral pores 10-10; rows separated mesially by five preanal scales.

Color of head uniform light tan with few minute dark spots; body ground color light gray with pattern of darker tans and browns; nuchal blotches confined mainly to neck, extending onto shoulder only short distance; dorsal spots indistinct, some appearing as irregular dark transverse strips; tail with several narrow dark bands; general over-all dorsal coloration faded, ventral scales light throughout.

Variation: In the eight adult specimens available for this study only minor variations were found in the diagnostic characters.

The size and placement of the temporal spines varied only slightly from that given above. The femoral pores vary in number from 5-6 to 11-11, the latter being that of the type specimen. Four to eight preanal scales separate the rows mesially. The dorsal ground color varies from a light tan to a medium gray, but is lighter than the general color of *P. p. calidiarum*.

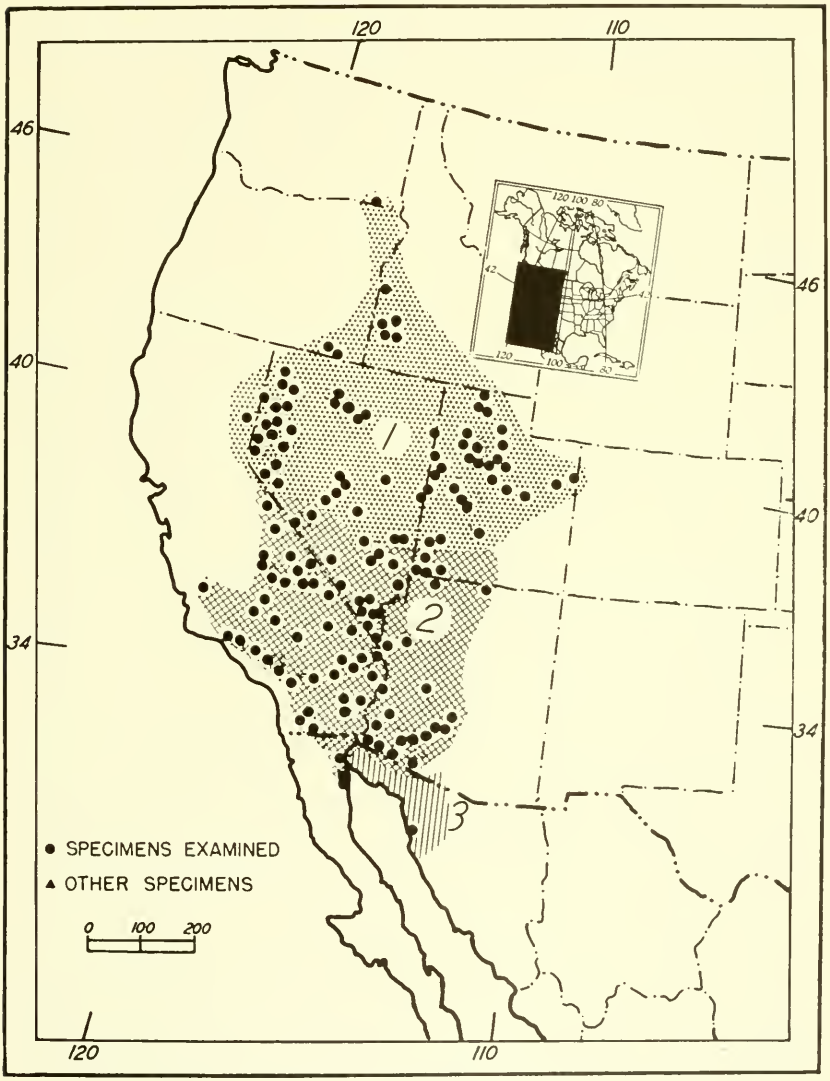

FIG. 3. Map showing the geographic distribution of the species *Phrynosoma platyrhinos*

1. *Phrynosoma p. platyrhinos* 2. *Phrynosoma p. calidiarum*
3. *Phrynosoma p. goodei*

General distribution: Western part of Sonora.

Locality records: SONORA. Álamo Muerto, NW of, (MVZ 10166). Puerto Libertad (SSNH 16693). (AMNH 69653-56); West Coast (USNM 8567a type & 8567b).

Phrynosoma m'callii (Hallowell)

Anota m'callii Hallowell, Proc. Acad. Nat. Sci. Philadelphia, vol. 6, 1852, p. 182; Hallowell, Sitgreaves' Expedition down the Zuni and Colorado Rivers, 1853, p. 127, pl. 10; Bocourt, Mission Scientifique Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 4, 1874, p. 230.

Doliosaurus m'callii Girard, United States Exploring Expeditions of the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes USN, vol. 20, Herpetology, 1858, p. 408; Baird, United States Mexican Boundary Survey under the order of Lieut. Col. W. H. Emory, Reptiles of the Boundary, vol. 2, 1859, p. 9, pl. 28, figs. 4-6; Cooper, Proc. California Acad. Sci., vol. 4, 1870, p. 67.

Phrynosoma maccallii Cope, Proc. Acad. Nat. Sci. Philadelphia, 1866, p. 310; Cope, Bull. U. S. Nat. Mus., no. 24, 1875, pp. 11, 65; Gentry, Proc. Acad. Nat. Sci. Philadelphia, 1885, p. 148.

Anota maccallii Cope, Report U. S. Nat. Mus. for 1898, (1900), p. 448, fig. 82; Bryant, Univ. California Publ. Zool., vol. 9, 1911, pp. 54, 55, pl. 7.

Phrynosoma m'callii Stejneger, N. Amer. Fauna, no. 7, 1893, p. 190; Van Denburg, Occas. Papers California Acad. Sci., no. 5, 1897, pp. 89, 100-101; Ditmars, Reptiles of the World, 1910, p. 151; Van Denburgh, Occas. Papers California Acad. Sci., ser. 4, vol. 3, 1912, p. 153; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 3, 1913, pp. 392, 406; Grinnell & Camp, Univ. California Publ. Zool., vol. 17, 1917, no. 10, p. 166; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 1917, p. 59; Hall & Grinnell, Proc. California Acad. Sci., ser. 4, vol. 11, 1919, p. 51; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, vol. 1, 1922, pp. 428-340, pl. 37; Stejneger & Barbour, Check List North American Amphibians and Reptiles, 2 ed., 1923, p. 62; Klauber, Bull. Zool. Soc. San Diego, no. 4, 1928, p. 4, and 1930, *idem*, no. 5, p. 4; Klauber, Copeia, 1932, no. 2, p. 100; Cuesta Terron, Anal. Inst. Biol., vol. 3, 1932, pp. 118-119; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 68; Klauber, Bull. Zool. Soc. San Diego, no. 11, 1934, p. 12; Smith, Trans. Kansas Acad. Sci., vol. 37, 1934, p. 287; Mosauer, Ecology, vol. 16, 1935, p. 19; Burt, Trans. Kansas Acad. Sci., vol. 38, 1936, p. 261; Klauber, Bull Zool. Soc. San Diego, no. 14, 1939, p. 95; Cowles, Science, NS., vol. 90, 1939, pp. 465-466; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed., 1939, pp. 74-75; Driver, Name That Animal, 1942, p. 346; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll. vol. 83, 1943, p. 93; Cowles, Bull. Amer. Mus. Nat. Hist., vol. 83, 1944, pp. 265-296; Smith, Handbook of Lizards, 1946, pp. 289, 308-10; Norris, Copeia, 1949, pp. 176-180; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, p. 355, and Bull. U. S. Nat. Mus. no. 199, 1950, pp. 99-100.

Anota m'callii Stephens, Trans. San Diego Soc. Nat. Hist., vol. 3, 1921, p. 62.

Taxonomic history: Hallowell (1852) described this species as *Anota m'callii*. Girard (1858) placed it in his subgenus *Doliosaurus* in the genus *Phrynosoma*. Cope (1900) again relegated it to the genus *Anota*. Stejneger (1893) dropped Girard's subgenus and used the name *Phrynosoma m'callii*, as have all subsequent writers except Bryant (1911). He pointed out that the supratemporal

fossae of this form were closed by a membranous bony growth and upon such evidence again referred it to *Anota*. Subsequent workers have been prone to disregard Bryant's generic allocation because it was based upon a single specimen.*

Diagnosis: Nostrils within the canthal lines; ventral scales smooth throughout; single row of enlarged gular scales on either side; a mid-dorsal dark line extending from head to base of tail; tympanum concealed; tail flattened.

Description: Head slightly longer than wide, rostrum forming a sharp angle at its union with frontal area; nares within the canthal lines, separated by a distance equal to diameter of nares; frontal scales irregular, those outlining the supraoccular fossae often slightly enlarged; superciliary ridge formed by seven slightly enlarged, pointed scales, and terminating posteriorly in a broad, short spine; occipital spines long and divergent; three temporal spines, last much larger than first; tympanum concealed by scaly integument; rostral slightly enlarged, broader than high and joined laterally by a series of eight or nine supralabials; infralabials inconspicuous, eight or nine in number, separated from chinshields by one or two minute sublabials; eight large serrate chinshields on each side, first two small, remainder subequal in size; single, slightly enlarged row of scales on either side of gular area; a few enlarged, pointed scales on the lateral neck area, these usually arranged in two distinct groups; back covered with small imbricate scales with larger keeled scales dispersed in more or less distinct rows; largest scales forming centers of three pairs of dark spots which parallel the vertebral column. Tail dorsoventrally flattened with two distinct rows of enlarged scales on its upper surface; two small lateral abdominal scale rows, second much smaller than first; a single row of conical scales bordering edge of tail; humerus with several rows of large, imbricate, keeled scales; femur bearing an anterior and a posterior row of slightly enlarged pointed scales; ventral scales smooth throughout; each femoral pore in the center of a single scale; 17-24 pores on each side, the rows separated mesially by from 3-10 preanal scales.

Dorsal ground color an ash-gray, with a distinct dark vertebral line from head to base of tail; several pairs of dark spots over back, each covering a single enlarged scale; several pairs of faint spots on

* Since this paper went to press, Norris and Lowe (Bull. Chicago Acad. Sci., vol. 9, no. 7, 1951, pp. 117-125) have, I believe, conclusively shown that this form should be retained in the genus *Phrynosoma*.

tail uniting into transverse bands toward its end; ventral surface uniform white or cream without dark markings.

Variations: The lateral abdominal scale rows are, in some specimens, reduced to near the size of the surrounding scales. The femoral pores vary from 17-24 on each side with from 3-10 preanal scales separating the rows. The dorsal ground color may vary with the substratum upon which the lizard lives, but in general it will be light cream with the pattern appearing faded. The dark vertebral line may be faded also.

Discussion: The habits of this moderate-sized lizard are not well known. It seems to be mostly, if not entirely, restricted to sandy situations as stated by Klauber (1939) and Norris (1949). Stebbins (1943) discusses the sand adaptations found in this and other lizards. The temperature tolerance has been discussed by Cowles (1939), Cowles and Bogert (1944), and Norris (1949). The active range of these lizards seems to lie between 36 and 37° C (temperatures on surface of sand) with a maximum of 41 to 42° C above which the lizard retreated below the surface of the sand.

The reproductive habits are little known. Norris (*op. cit.*) collected a specimen on 15 May, 1948, which, when dissected, was found to contain seven fully developed eggs. The eggs contained fluid yolk but no detectable embryos.

Distribution: The general distribution of this species is concentrated in the extreme desert areas of southeastern California, the northeastern part of Baja California, the extreme southwestern corner of Arizona and the extreme northwestern part of Sonora. The specimens reported by Klauber from west of Needles, San Bernardino Co., California, were found to be *P. p. calidiarum.*

Locality records: CALIFORNIA. *Imperial Co.:* Benson's Dry Lake, 4 mi. E (LMK 33940); Coyote Mts. (SSNH 13922); Coyote Wells (MVZ 1001); Harpers Well (LMK 23094); Holtville (LMK 1294); Kane Spring (Klauber, 1932); Midway Well (LMK 20174); Plaster City (SSNH 13924), 4 mi. W (LMK 34084); Salton Lake (Sea) (USNM 19095); Salton Park (MVZ 1007, 1019); Seeley (Klauber, 1932); Signal Mt. (LMK 23094); Springers (LMK 28521); Westmoreland (KU 6998). *Riverside Co.:* LaQuinta, 2 mi. E (LMK 23368); Mecca (MVZ 447-450); Palm Springs (LMK 39766, 39765), (MVZ 7063). *San Diego Co.:* Benson's Dry Lake (LMK 22734-38, 22847-48, 23014-15, 23626-30, 23808, 23820-21, 23974-77, 24033-34, 26748, 26888, 26958-59, 27233-37, 27402, 27889, 31621-26, 32990,

33860, 33940), (SSNH 16513-15, 17168); Borrego Valley (LMK 4513, 5810, 33165).

Mexico. *Baja California:* Horseshoe Bend, Colo. River (USNM 15976); Laguna Salada, west side (LMK 32034); Yuha Basin, 3 mi. S United States Border (LMK 7041). *Sonora:* Colorado River, east bank, 5 mi. S United States border (Smith and Taylor, 1950); no specific locality (Bryant, 1911).

Arizona. *Yuma Co.:* Desert of Colo. and Gila River (USNM 162, 4 spec.); Ft. Yuma (USNM 15955); Yuma, 25 mi. W (KU 21930-31), Sandhills E of (CAS 33486-87, 33654), not examined by me.

Phrynosoma modestum Girard

Phrynosoma modestum Girard, *in* Stansbury's Exploration of the Valley of Great Salt Lake Utah, 1852, pp. 361, 365, pl. 6, figs. 4-8; Baird & Girard, Proc. Acad. Nat. Sci. Philadelphia, vol. 6, 1852, p. 69; Hallowell, Sitgreaves' Expedition down the Zuni & Colorado Rivers, 1853, p. 145; Cope, Proc. Acad. Nat. Sci. Philadelphia, 1866, pp. 302-303; Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 4, 1874, p. 232; Cope, Bull. U. S. Nat. Mus. no. 1, 1875, p. 49; Yarrow, Report upon the Geography and Geology Survey West of the 100th Meridian in charge of First Lieut. Geo. M. Wheeler, vol. 5, Zoology, 1875, p. 594; Cope, Proc. Acad. Nat. Sci. Philadelphia, 1883, pp. 10, 12; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, pp. 11, 64 (*part.*); Cragin, Bull. Washburn Lab., vol. 1, 1884, p. 6; Gentry, Proc. Acad. Nat. Sci. Philadelphia, 1885, p. 148; Boulenger, Catalogue of the Lizards in the British Museum Natural History, vol. 2, 1885, p. 248; Cope, Proc. Amer. Phil. Soc., vol. 23, 1886, p. 282; Cope, Bull. U. S. Nat. Mus., no. 32, 1887, p. 38; Garman, Bull. Essex Inst., vol. 19, 1887, p. 12; Günther, Biologia Centrali-Americana, Reptiles and Batrachia, 1890, p. 79; Boulenger, Proc. Zool. Soc. London, 1890, p. 78; Cope; Proc. Acad. Nat. Sci. Philadelphia, 1892, p. 335; Van Denburgh, Proc. California Acad. Sci., ser. 2, vol. 6, 1896; p. 342; Cockerell, Amer. Nat. vol. 30, 1896, p. 327; Brown, Proc. Acad. Nat. Sci. Philadelphia, vol. 55, 1903, pp. 546-552; Bailey, N. Amer. Fauna, no. 25, 1905, p. 43; Gadow, Proc. Zool. Soc. London, vol. 194, 1905, p. 213; Ditmars, The Reptile Book, 1907, p. 156; Strecker, Baylor Univ. Bull., vol. 12, no. 1, 1909, p. 13; Ditmars, Reptiles of the World, 1910, p. 151; Gadow, Zool. Jahrb. vol. 29, 1910, p. 706; Stone, Proc. Acad. Nat. Sci. Philadelphia, 1911, p. 229; Bryant, Univ. California Publ. Zool., vol. 9, no. 1, 1911, p. 5; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 3, 1913, p. 393; Strecker, Baylor Univ. Bull., vol. 18, no. 4, 1915, p. 23; Stejneger & Barbour, Check List of the North American Amphibians and Reptiles, 1917, p. 59; Weese, Amer. Nat. vol. 53, 1919, pp. 33-54; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, vol. 1, 1922, pp. 430-433, pl. 38; Strecker, Sci. Soc. San Antonio, Bull. no. 4, 1922, p. 31; Stejneger & Barbour, Check List of the North American Amphibians and Reptiles, 2 ed. 1923, p. 63; Van Denburgh, Proc. California Acad. Sci., ser. 4, vol. 13, 1924, pp. 191, 210; Burt & Burt, Journ. Washington Acad. Sci., vol. 19, no. 20, 1929, p. 454; Cuesta Terron, Ann. Inst. Biol., vol. 3, 1932, pp. 119-120, fig. 18; Stejneger & Barbour, Check List of the North American Amphibians and Reptiles, 3 ed., 1933, pp. 68-69; Smith, Trans. Kansas Acad. Sci., vol. 37, 1934, pp. 287-289, 290, pl. 11, fig. 3; Burt, Amer. Midl. Nat., vol. 16, 1935, p. 324; Bogert & Oliver, Bull. Amer. Mus. Nat. Hist., vol. 83, 1935, pp. 315, 324; Smith, Univ. Kansas Sci. Bull., vol.

22, 1935, p. 144; Dunn, Proc. Acad. Nat. Sci. Philadelphia, vol. 88, 1936, p. 475; Burt, Trans. Kansas Acad. Sci., vol. 38, 1936, pp. 261, 300, 305; Gloyd, Bull. Chicago Acad. Sci., vol. 5, 1937, p. 113; Little & Keller, Copeia, no. 4, 1937, pp. 219-220; Stejneger & Barbour, Check List of the North American Amphibians and Reptiles, 4 ed. 1939, p. 75; Driver, Name That Animal, 1942, p. 348; Smith & Mittleman, Trans. Kansas Acad. Sci., vol. 46, 1943, p. 245; Marr, Amer. Midland Nat., vol. 32, 1943, p. 482; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll. vol. 93, 1943, p. 93; Schmidt & Smith, Zool. Ser. Field Mus. Nat. Hist., vol. 29, 1944, pp. 78, 84; Schmidt & Owens, Zool. Ser. Field Mus. Nat. Hist., vol. 29, 1944, p. 106; Smith & Laufe, Trans. Kansas Acad. Sci., vol. 38, 1945, p. 337; Smith Handbook of Lizards, 1946, pp. 311-313; Maslin, Univ. Colorado Mus. Leaflet, no. 3, 1947, pp. 5, 12; Lowe, Herpetologia, vol. 4, 1947, p. 77; Smith & Taylor, Kansas Sci. Bull. vol. 33, pt. 2, 1950, p. 359; Bull. U. S. Nat. Mus., no. 199, 1950, p. 101.

Doliosaurus modestus Girard, United States Exploring Expeditions of the years 1838, 1839, 1840, 1841, 1842, under the Command of Charles Wilkes USN, vol. 20, Herpetology, 1858, p. 409; Baird, United States Mexican Boundary Survey, under the order of Lieut. Col. W. H. Emory, Reptiles of the Boundary, vol. 2, 1859, p. 10; Baird, Reptiles of the Pacific Rail Road Survey, vol. 10, 1859, p. 38.

Anota modesta Cope, Amer. Nat., vol. 30, 1896, p. 1014; Cope, Report U. S. Nat. Mus. for 1898 (1900), p. 437, fig. 78; Stone & Rehn, Proc. Acad. Nat. Sci. Philadelphia, 1903, p. 32; Ruthven, Bull. Amer. Mus. Nat. Hist., vol. 23, 1907, pp. 550-552; Mearns, Bull. U. S. Nat. Mus., no. 56, 1907, p. 115; Ellis & Henderson, Univ. Colorado Studies, vol. 10, 1913, p. 75.

Phrynosoma platyrhynus Herrick, Terry & Herrick, Bull. Univ. New Mexico, vol. 1, 1899, p. 136, pl. 10, fig. 18.

Taxonomic history: Girard (1852:361) described and named this species from specimens in the United States National Museum taken by Gen. Churchill (No. 163) "from the Rio Grande, west of San Antonio", and by Col. Graham (No. 164, 8 specimens) "from San Antonio to El Paso." Later Girard (1858) divided this genus into four subgenera and relegated this species to his subgenus *Doliosaurus*. Bocourt (1874) also using subgenera placed *modestum* in his subgenus *Phrynosoma*. Cope (1896 and 1900) placed it, along with four other species, in a separate and distinct genus *Anota*, which was characterized by concealed tympana. Subsequent workers, finding the condition of the tympanum in *modestum* varied from complete concealment to complete exposure, chose to disregard Cope's arrangement, using the name *Phrynosoma modestum*.

The type locality, has recently been restricted to Las Cruces, Dona Ana Co., New Mexico, by Smith and Taylor (1950a).

Diagnosis: This small species can be identified by the following characters: absence of the lateral abdominal fringe; moderate development of the dorsal scales, round cylindrical tail; chinshields in contact with the infralabials.

Description: Head as broad as long; rostrofrontal angle abrupt; nostrils moderately large and situated between the canthal lines;

posterior margin of head bearing two occipital and two temporal spines, latter equal to or projecting beyond occipitals; superciliary spine small; chinshields increasing in size posteriorly, penultimate largest, all in contact with infralabials; gular scales small, subequal; one slightly enlarged row in contact with chinshields; tympanum exposed or concealed; neck patches inconspicuous; dorsal scales mainly granular, a few enlarged, keeled scales scattered over back and tail; lateral abdominal fringe absent; ventral scales moderately large and smooth; enlarged postanal scales present in males; seven to thirteen femoral pores on each side, rows separated mesially by as many as five preanal scales; tail reduced abruptly behind base, forming gradually tapering cylinder; lateral fringe absent on tail.

General color light cream appearing bleached; pattern usually apparent and distinctive; ground color varying from light gray to light brown; several dark spots visible on dorsum, most prominent ones on lateral surface of neck; dark groin spots often extending forward to axilla; tail traversed by several dark bands; ventral scales generally without dark spots.

Variation: The degree to which the tympanum is concealed varies greatly among individuals of any given population. In some specimens the tympanum is completely hidden by a scaly integument and in others it is partly exposed and in others it is completely exposed. The tympana on opposite sides of the head of a single individual may differ in concealment to a degree nearly equal to that found in the species as a whole. The number of pores on the ventral surface of each femur varies from minimum of seven to as many as thirteen, the rows being either continuous across the preanal area or separated by a maximum of five scales. The length of the row of pores seems to have no influence on the number of intervening preanal scales; specimens with as many as twelve pores in each row have the rows separated mesially by five preanal scales.

In most specimens the dorsal pattern is faint but in some is greatly darkened. This is especially true of the blotches on the neck and groin. These blotches may meet each other and form dark lateral stripes, which may expand dorsally and approach the vertebral line. The ventral scales are usually void of dark pigment but may possess a random sprinkling of dark flecks.

Discussion: This small, bleached form is not closely related to any other species in the genus. Although not so specialized as

some species, it is certainly unique in the presence of a cylindrical tail and absence of a lateral fringe.

Distribution: The general distribution of this species extends from the central and southern parts of Texas, west through southern New Mexico, and the southeastern part of Arizona, south through the northeastern part of Sonora, most of Chihuahua, southeastward through the northern third of Durango, the northern part of Zacatecas and northeastward through Nuevo León.

Locality records: TEXAS. *Bexar Co.:* San Antonio (Baird and Girard, 1852). *Brewster Co.:* Alpine (USNM 33000); Big Bend area (AMNH 62981); Lone Mt. (USNM 103669); Sanderson, 58 mi. W (MVZ 36713). *Culberson Co.:* Guadalupe Mts. (USNM 32999); Between Guadalupe Mts. and Rio Pecos (USNM 184). *El Paso Co.:* El Paso City (AMNH 15050, 28386, 28649); Ft. Bliss (USNM 83119-20), (AMNH 43287-88); no specific locality (USNM 58182), (KU 15394). *Howard Co.:* Big Springs, 1 mi. E (MVZ 38422), 10 mi. SW (MVZ 38423). *Jeff Davis Co.:* Davis Mts. (USNM 32996). *Llano Co.:* Llano Estacado (USNM 186). *Motley Co.:* Flomot, 3 mi. W (AMNH 67858); Matador, 18 mi. NW (AMNH 67859). *Pecos Co.:* Ft. Stockton (USNM 5176). *Reeves Co.:* Pecos City (USNM 30877); Tayoh (USNM 32997). *Taylor Co.:* Camp Barkley (BYU 6915, 6058-59).

NEW MEXICO. *Bernalillo Co.:* Albuquerque (USNM 37962-4, 32993-5), (AMNH 15197), (KU 11310-14), 10 mi. N (MVZ 33724). *Chaves Co.:* Roswell, 7 mi. E (USNM 93008), 15 mi. W (USNM 32998). *Dona Ana Co.:* Jornada Exp. Range (USNM 100887); Los Cruces (USNM 22320); Rope Springs (USNM 102254). *Eddy Co.:* Carlsbad, 5 mi. N (USNM 93035). *Grant Co.:* Dog Springs (USNM 21014). *Guadalupe Co.:* Between Anton Chico and Cuesta (USNM 174). *Luna Co.:* Silver City, 29 mi. SE (KU 6555). *Otero Co.:* Alamogordo (AMNH 560-66). *Sante Fe Co.:* San Ildefonso (USNM 8511). *Socorro Co.:* Magdelina Mts. (KU 474); San Marcial (Burt, 1935); no specific locality (KU 473). *San Miguel Co.:* no specific locality (Van Denburgh, 1924). *Sierra Co.:* no specific locality (Van Denburgh, 1924).

ARIZONA. *Cochise Co.:* Bowie (USNM 8590); Dos Cabezo (Gloyd, 1937); San Pedro River (USNM 21021).

MEXICO. *Chihuahua:* Ahumada, 11 mi. S (USNM 104687); Chihuahua (city) (USNM 46655), 4 mi. NW (KU 28069); Guzman (Stone, 1911); Júarez (Gadow, 1905); Near Janos (Cope, 1900); Near Progresso Río Santa Maria (USNM 104688-91); Santa Marcia

(USNM 47180-83); Samalayuca, 8 mi. N (AMNH 68432). *Coahuila:* Agua Nueva (Cope, 1900), Álamo de Parros (USNM 177); Allende (Schmidt & Owens, 1944); Buena Vista (Cope, 1900); Cabos (AMNH 68862); Castañuelas (Cope, 1900); Cuatro Ciénegas (Schmidt & Owens, 1944); Hermanas (Schmidt & Owens, 1944); Los Delícias (AMNH 67384), 17 mi. S (AMNH 67383), 5 mi. E (AMNH 67384); Monclova (USNM 67833); Múzquiz

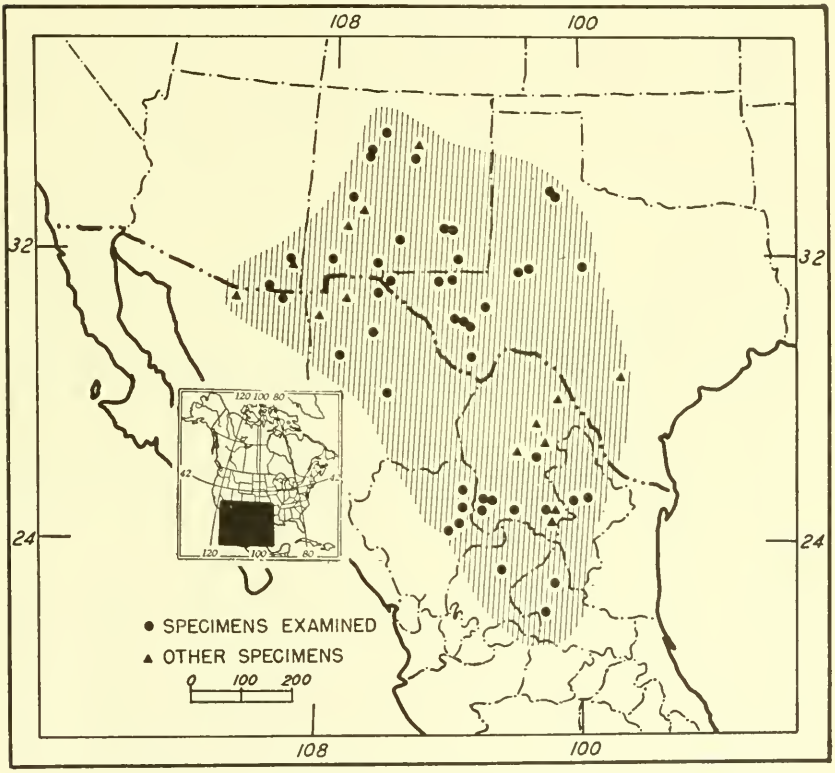

FIG. 4. Map showing the geographic distribution of the species *Phrynosoma modestum.*

(Smith & Mittleman, 1943); Palau (Schmidt & Owens, 1944); Saltillo (Garman, 1887), 1½ mi. W (EHT-HMS 10443); San Pedro (Garman, 1887). *Durango*: Bermejillo, 25 mi. N (KU 19247); La Loma, 7 mi. S (EHT-HMS 10442); Pedriceña (USNM 105313-14); San Juan del Río (AMNH 68340); Between Lerdo and La Goma (USNM 105312). *San Luis Potosí*: Hacienda La Parada (USNM 47211); San Luis Potosí (city), 130 km. N (EHT-HMS 23979, 23968, 23971). *Nuevo León:* Pesquiera Grande (USNM

180, 3 specimens); Santa Caterina (USNM 47837-42). *Sonora*: Los Nogales (Smith & Mittleman, 1943); Nariz Temporal (Mearns, 1907); Sierra de La Nariz (USNM 166-167). *Zacatecas:* La Colorado, 3 mi. W (KU 19246).

Phrynosoma coronatum blainvillii Gray

Phrynosoma blainvillii Gray, Zoology of Beechey's Voyage, 1837, p. 96, pl. 29, fig. 1; Gray, Catalogue of the Species of Lizards in the British Museum (Natural History), 1845, p. 228; Stejneger, N. Amer. Fauna., no. 7, 1893, p. 187; Van Denburgh, Proc. California Acad. Sci. ser. 2, vol. 4, 1895, p. 118; Van Denburgh, Proc. California Acad. Sci., ser. 2, vol. 5, 1896, p. 1005; Van Denburgh, Occas. Papers California Acad. Sci. no. 5, 1897, p. 91; McLain, Critical Notes on a Collection of Reptiles from the West Coast of North America, 1899, p. 8; Meek, Field Columbian Mus., Zool. Ser., vol. 7, 1906, p. 12; Grinnell & Grinnell, Throop Institute Bulletin, no. 35, 1907, p. 26; Grinnell, Univ. California Publ. Zool. vol. 5, 1908, p. 162; Van Denburgh, Proc. California Acad. Sci., ser. 4, vol. 3, 1912, pp. 148-152; Hurter, First Ann. Rep. Laguna Marine Lab. 1912, p. 67; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 1917, p. 57; Nelson, Mem. Nat. Acad. Sci., vol. 16, 1921, pp. 59, 114.

Phrynosoma coronatum Hallowell, *in* Sitgreaves' Expedition Down Zuni and Colorado Rivers, 1853, p. 122; Lockington, Amer. Naturalist, 1880, p. 295; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 70 (*part.*); Gentry, Proc. Acad. Nat. Sci. Philadelphia, 1885, p. 143 (*part.*); Cope, Report U. S. Nat. Mus. for 1898, (1900), p. 430, fig. 76 (*part.*); Meek, Field Columbian Mus., Zool. Ser., vol. 7, 1906, p. 12; Ditmars, The Reptile Book, 1907, p. 152, pls. 46, figs. 12, 16, 49, fig. 2 (*part.*); Bryant, Univ. California Publ. Zool., vol. 9, 1911, p. 18 (*part.*).

Batrachosoma coronatum Girard, United States Exploring Expedition of the Years 1838, 1839, 1840, 1841, 1842, under the Command of Charles Wilkes USN., vol. 20, Herpetology, 1858, p. 400, pl. 20, figs. 10-13; Aug. Duméril & Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 1, 1870, pl. 12, fig. 10; Bocourt, 1874, *idem*, livr. 4, p. 239, (*part.*).

Phrynosoma blainvillei Cope, Bull. U. S. Nat. Mus., no. 1, 1875, p. 49 (*part.*); Cope, Proc. Acad. Nat. Sci. Philadelphia, 1883, pp. 28, 30; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 70 (*part.*); Cope, Report U. S. Nat. Mus. for 1898, (1900), p. 423, fig. 74 (*part.*); Stephens, Trans. San Diego Soc. Nat. Hist. vol. 3, no. 4, 1921, p. 62.

Phrynosoma blainvillii blainvillii Bryant, Univ. California Zool. vol. 9, 1911, pp. 5, 19, 29, pl. 4; Atsatt, Univ. California Publ. Zool., vol. 17, 1913, p. 164; Cowles, Journ. Entomol. Zool., Pomona College, vol. 12, 1920, p. 66; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 11, 1921, pp. 51, 62; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, vol. 1, 1922, pp. 388-395, pl. 32; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 2 ed., 1923, p. 60; Klauber, Bull. Zool. Soc. San Diego, no. 4, 1928, p. 3 and *idem*, no. 5, 1930, p. 4; Bogert, Bull. Southern California Acad. Sci., vol. 29, 1930, p. 7; Klauber, Copeia, no. 2, 1932, p. 123; Stejneger & Barbour, Check List North American Amphibians and Reptiles, 3 ed., 1933, p. 66; Klauber, Copeia, no. 2, 1936, pp. 103-106; Wood, Copeia, no. 3, 1936, p. 177; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed. 1939, p. 72; Smith, Ann. Carnegie Mus., vol. 27, 1939, p. 314; Klauber, Bull. Zool. Soc. San Diego, no. 14, 1939, pp. 93-94; Cowles, Science, NS, vol. 90, 1939, pp. 465-466; Burleson, Copeia, 1942, pp. 246-248; fig. 2 (unnumbered); Driver, Name That Animal, 1942, p. 348; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll. vol. 93, 1943, p. 91; Cowles, Bull. Amer. Mus. Nat. Hist., vol. 83, 1944, pp. 265-296.

Phrynosoma coronatum blainvillii Linsdale, Univ. California Publ. Zool., vol. 38, 1932, pp. 349, 368 (*part.*); Burt, Amer. Midl. Nat., vol. 14, 1933, pp. 243-244; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, pp. 357, 375; Bull. U. S. Nat. Mus. no. 199, 1950, p. 103.

Taxonomic history: Blainville's Horned Lizard was described in 1839 by Gray from a specimen collected in "California" by Botta and given to Gray by de Blainville after whom it was named. Its conspecificity with *frontale* was first suspected by Van Denburgh (1897) and was demonstrated by Bryant (1911). Linsdale (1932) recognized only the species *coronatum* reducing *blainvillii* to subspecific status. This met with considerable objection, resulting in the controversy commented upon in the discussion of this form.

Diagnosis: Three or more rows of enlarged gular scales on each side; five posteriorly curved temporal spines; frontal scales large, smooth and rounded.

Description: Head wider than long; frontal area flat; frontal scales large convex and smooth; superciliary ridges distinct, terminating posteriorly in broad, short superciliary spine; occipital shelf bearing four enlarged tubercles; occipital spines large, parallel and curved slightly downward; small interoccipital spine; temporal shelf moderately expanded, bearing five enlarged spines; temporal spines increasing in size posteriorly; terminal spine subequal to occipital spine; nostrils on canthal lines; internasal distance equal to four times diameter of single nostril; supralabials small, inconspicuous; infralabials small, in contact with the chinshields; chinshields five, increasing in size posteriorly; subrictal above line of chinshields, postrictal large, cone-shaped; four rows of enlarged gular scales on each side; outer row largest; two lateral neck patches of enlarged, pointed, soft spines; dorsal scales minute, imbricate and nonkeeled; numerous large, keeled scales scattered over back; two lateral abdominal scale rows, upper row largest, extending from shoulder above arm to groin, lower row limited to central part of abdomen; three large scales on femur; several rows of heavily keeled scales on each humerus; tail with two lateral rows and numerous dorsal, enlarged, keeled scales; ventral scales smooth; femoral pores 15-15.

Dorsal ground color light gray; nuchal blotches large and distinct, dorsal markings moderately wide, irregular bars; five bars traversing tail; frontal area yellowish-tan; temporal and lateral area light gray; venter light tan with light brown spots.

Variation: Being a poorly differentiated form of *coronatum*, this subspecies shows many affinities to *frontale*. The frontal scales are

the only authentic character that will segregate this form from those to the north or south.

Discussion: Two general ideas have been held by recent workers concerning the relationships of the mainland forms of the *coronatum-blainvillii* complex of the horned lizards. The first idea is that *blainvillii* and *coronatum* are distinct species, each with subspecies. The second idea is that there is only one species, *Phrynosoma coronatum,* of which the other forms are subspecies. Linsdale (1932) was the first to suggest that all forms concerned should be considered as subspecies of *P. coronatum,* listing the forms from south to north, as: *P. coronatum coronatum, P. coronatum jamesi, P. coronatum blainvillii* and *P. coronatum frontale.* He considered specimens from northern Baja California as intergrades between *P. c. jamesi* and *P. c. blainvillii.* Klauber (1936) studied these forms, took exception to Linsdale's arrangement, and suggested that two distinct species were involved: The first *P. blainvillii* in which he placed *P. b. blainvillii* and *P. b. frontale* and the second, *P. coronatum* in which he placed *P. c. jamesi* and *P. c. coronatum.* He placed specimens from the upper part of Baja California in a southern population of *P. b. frontale.* Tevis (1944), with additional specimens, supported Linsdale's idea of a single species. The material used by the above three workers plus additional material has been studied by me. The resulting data supports the idea that there is a single mainland species with several subspecies. As Linsdale (*op. cit.*) suggested, a trend of characters exists from *coronatum* through *jamesi* to *blainvillii.* Klauber (*op. cit.*) also observed this trend but noted that specimens of *c. coronatum* differed more from the San Diegan specimens of *P. blainvillii* (= *P. c. blainvillii*) than they did from the more northerly specimens of *P. blainvillii* (= *P. c. frontale*) and therefore thought that the geographic sequence of the trend was discontinuous. This is definitely the case. However, elsewhere (p. 107) in his paper Klauber states, "I therefore conclude that *nelsoni* is invalid and that *P. blainvillii frontale,* which must be the parent form of *blainvillii,* occupies two distinct areas separated by the mildly differentiated race, *P. blainvillii blainvillii.*"

My own study convinces me that the differentiation of *blainvillii* from *frontale* is as Klauber described it but I do not agree with him that two species are involved. If the dispersal onto the peninsula was from the north, as is probable, the parent stock of *blainvillii* (which is *frontale*) should have more characters in common with the Cape form *coronatum* than would its offshoot *blainvillii.* This being the case I, therefore, believe that the data indicate con-

specificity of the two groups rather than the opposite as held by Klauber.

I have found characters to distinguish the northern population of *frontale* from the southern population. (See diagnosis and Table 4.) My arrangement of these forms is as follows:

P. coronatum coronatum, Cape region

P. coronatum jamesi, between lat. 26°20′ and 28°40′

P. coronatum schmidti, between lat. 28°40′ to near 31°50′ and Cedros Island

P. coronatum blainvillii, northern part of Baja California and the southern counties of California

P. coronatum frontale, from southern to central California

P. cerroense, Cedros Island

General Distribution: Southernmost counties of western California and the very northern part of Baja California.

Locality records: California. *Imperial Co.:* no specific locality (Klauber 1934). *Los Angeles Co.:* Azusa, 1 mi N (AMNH 66279); Big Rock Creek (AMNH 68495-97); Claremont, 1½ mi. NW (MVZ 36312); Devils Punch Bowl (Bogert, 1930); Glendale (LMK 4863-64); La Crescenta (Van Denburgh, 1922); Lankershim, 1 mi. E (MVZ 7061); Pasadena (MVZ 852, 2413, 3558, 4799), (AMNH 58974); Placerita Cañon (USNM 54905); (LMK 4428); Rio Los Angeles, Dyke (AMNH 49968-69); San Gabriel Mts. (MVZ 4249), (USNM 44878-79); San Gabriel River, near Azusa (Van Denburgh, 1922); San Pedro (SSNH 14184); Santa Anita, 1½ mi. W (MVZ 25220); Sierra Madre (MVZ 2447, 4254); Valyermo, 1 mi. NW (LMK 40004); no secific locality (USNM 69778-79), (KU 9538-29). *Orange Co.:* Capistrano (USNM 44853), (LMK 31520); Laguna Beach (Van Denburgh, 1922); Santa Ana (Van Denburgh, 1922). *Riverside Co.:* Anza, 2½ mi. E (LMK 23375); Coahuila, 2 mi. W (LMK 23374); Coahuila Indian Reservation (LMK 28694-96); Elsinore (Klauber, 1932); March Field (SSNH 14179); Moreno (SSNH 12103-04); Nuevo, (SSNH 12009); Perris (LMK 2721); Ribbon wood, 2 mi. W (LMK 31519), 7 mi. W (LMK 33307); Temecula (Klauber, 1932). *San Bernardino Co.:* Adelanto, 20 mi. S (LMK 39914), 10 mi. S (LMK 40003); Bush, 6 mi. N (LMK 39903); Cactus Flats (LMK 27328); Cajon Pass (McLain, 1899); Colton, Reche Canyon (MVZ 22, 24, 25, 59, 60); Clark's Ranch (MVZ 858), (LMK 26406); Grapeland (Stanford 1616-14); Hesperia (SSNH 11219-20); Lytle Creek (Van Denbugh, 1922); Ontario (MVZ 31705); Redlands (LMK 23705); San Bernardino, 3 mi. N (MVZ 29381), (USNM 42133), (AMNH 20647-49); San Bernardino Mountains, Pipes Canyon (LMK 39762-

63), Pipee Canyon (LMK 39786); Santa Ana Canyon (MVZ 859); Santa Ana River (MVZ 704), South Fork (MVZ 860); Seven Oaks (MVZ 857); Shandon Hills (MVZ 39567); Sheep Creek (MVZ 39565); Swartout Canyon (Van Denburgh, 1922); Warren's Well (Van Denburgh, 1922); no specific locality (USNM 56863). *San Diego Co.:* Adobe Falls (Burt, 1933); Alpine (SSNH 15570); Ballena (SSNH 13917); Banner (LMK 20953); Barona Ranch (LMK 28623-24); Bonsall (LMK 27258); Boulder Creek (LMK 39392); Boulevard (LMK 26841); Cameron Ranch (USNM 21971); Campo (MVZ 381), (USNM 21973, 21993), (USNM 20483-85); Cuyamaca Lake (LMK 31473), 3 mi. SE (SSNH 18286); Chihuahua Mts. (McLain, 1899); Deerhorn Flats, (LMK 572-573); Dehesa (LMK 29016); Del Dios (LMK 23625, 28485); Dulzura (MVZ 382), Stanford 7919-20, (SSNH 11908); El Cajon (Stanford 7923-24); El Capitan (LMK 21253-54); El Nido (USNM 21965-67); Escondido (SSNH 11909-10, 11992-95); Escondido Reservoir (MVZ 872); Flinn Springs (LMK 1942); Gray's Ranch (USNM 21072); Gulion (MVZ 634); Hodges Dam (LMK 25449); Hot Springs Mts. (SSNH 17570); Jacumba Hot Springs (USNM 21981-91), (LMK 33862), (SSNH 11865), 4 mi. W (LMK 33861); Jamacha (LMK 585); Julian (Van Denburgh, 1922); Kitchen Creek (LMK 39775); Laguna Mountain (LMK 29017, 29079, 31619); Lake Side (USNM 53698-99), (LMK 4344, 27130); La Jolla (MVZ 43485-89), (LMK 25441); La Mesa (USNM 53688-91), (LMK 31233); La Posta (SSNH 13928); Lemon Grove (Stanford 7922); Mesa Grande (Van Denburgh, 1922); Monument 285 (SSNH 13918); Moretti's (LMK 31430); National City (MVZ 43502); Oak Grove (LMK 1848); Ocean Side (USNM 44861); Palm City (LMK 23953); Pine Hills (LMK 35191); Point Loma (SSNH 11216-18); Poway (Klauber 1932); Rainbow (Klauber, 1932); Rincon (LMK 575); Rosedale (Klauber, 1932); Ramona (LMK 27257, 31995), 4 mi. W (LMK 39851); San Diequito Valley (USNM 53694-97); San Diego (MVZ 43480, 43496, 43503), (BYU 8035-37, 8046), (USNM 157, 10779, 13893, 13948, 14587, 14777, 53692-93, 53700-02, 54365, 55105), (LMK 25788, 27409), (SSNH 11309-10, 11695); San Felipe Valley (LMK 8614, 26957, 27407); San Pasqual (LMK 4429); Shady Dell (LMK 7614); Scissor Crossing, 2 mi. W (LMK 31934); State College (LMK 39393); Santa Ysabel (LMK 39391); Sun Crest (LMK 37249), (SSNH 13302); Sutherland (LMK 20877); Tia Juana (USNM 21968-70, 21980); Tubb's Spring (SSNH 13367); Twin Oaks (USNM 16997); Valley

Center (SSNH 27529); Vista (LMK 4343); Warner's Pass (MVZ 1041); Witch Creek (SSNH 11308). *Riverside Co.*: Anza, 4 mi. W (LMK 39776); Banning (USNM 75137-38); Coahuila (=Cahuilla) (LMK 40060); Cabazon (Atsatt, 1913); Eden Hot Springs (LMK 27299); Elsinore (SSNH 13916); Helmet Valley (Van Denburgh, 1897); Keen Camp, 2 mi. W (LMK 25817); Kenworth (Van Denburgh, 1922); Oak Springs (Atsatt, 1913); Perris Valley (Van Denburgh, 1922); Reche Canyon (Van Denburgh, 1922); Riverside (Van Denburgh, 1922); Sage (LMK 10912, 27325); San Jacinto (Van Denburgh 1922); San Jacinto Mts. (USNM 44854); Temescal Mts. (Van Denburgh, 1922); Vallenista (Atsatt, 1913); Val Verde (LMK 23702).

Baja California. Alaska, 15 mi. W (SSNH 16012); Ensenada (Van Denburgh, 1922), 13 mi. S (LMK 23703-04); Laguna Hansen (LMK 27408); Lake Faustina (LMK 31446); Nachoguero Valley (Van Denburgh, 1922); Neji (LMK 23454), 6 mi. N (LMK 23445); Ojos Negros (USNM 37583), (LMK 23445-51, 27400); Pacific Coast, Lower California (USNM 21462); Punta Banda (LMK 26956); San Pedro (LMK 10410); San Rafael Valley, Wassom's Ranch (Van Denburgh, 1922); San Miguel Mission (LMK 23452); San Salado (Meeks, 1905); San Vincente, 3 mi. N (LMK 32128); Tecate (LMK 39063), 10 mi. E (SSNH 16013); Tijuana, 28 mi. S (LMK 38263); Valladeris (MVZ 9777); Valentín, 5 mi. E (LMK 23453).

Phrynosoma coronatum coronatum (Blainville)

Agama (*Phrynosoma*) *coronata* Blainville, Nouv, Ann. Mus. Hist. Nat. Paris, vol. 4, 1835, pp. 52-54, pl. 25, figs. 1a-c.

Phrynosoma coronatum Aug. Duméril & Bibron, Érpetologie Générale, vol. 4, p. 318; Duméril & Duméril, Catalogue Méthodique Collection Reptiles du Muséum d'Histoire Naturelle de Paris, 1851, pp. 78-80; Aug. Duméril & Bocourt, Mission Scientifique au Mexique et dans l'Amerique Centrale, Études sur les Reptiles, livr. 1, 1870, pl. 12, fig. 10; Bocourt, *idem*, livr. 4, 1874, p. 239 (*part.*); Cope Proc. Acad. Nat. Sci. Philadelphia, 1866, p. 312; Cope, Bull. U. S. Nat. Mus., no. 1, 1875, pp. 50, 93; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 39; Stejneger, N. Amer. Fauna, no. 7, 1893, p. 187; Van Denburgh, Proc. California Acad. Sci., ser. 2, vol. 4, 1894, p. 296; Van Denburgh, Proc. California Acad. Sci., ser. 2, vol. 5, 1895, p. 115; Cope, Rept. U. S. Nat. Mus. for 1898 (1900), p. 430 (*part.*); McLain, Contributions to the Neotropical Herpetology, 1899, p. 2; Mocquard, Nouv. Arch. Mus. Hist. Nat. Paris, ser. 4, vol. 1, 1899, p. 314; Ditmars, Reptiles of the World, 1910, pp. 151-153 (*part.*); Bryant, Univ. California Publ. Zool., vol. 9, 1911, p. 5; Stejneger & Barbour, Check List North American Amphibians and Reptiles, 1917, p. 58; Van Denburgh & Slevin, Proc. California Acad. Sci., vol. 11, 1921, pp. 51, 62; Nelson, Mem. Nat. Acad. Sci., vol. 16, 1922, pp. 114, 115; Cuesta Terron, Mem. Y. Rev. Soc. Cient. Antonio Atzate, vol. 39, 1921, pp. 165-166; Van Denburgh, Occas. Papers. California Acad. Sci., no. 10, vol. 1, 1922, pp. 403-406; Stejneger & Barbour,

Check List of North American Amphibians and Reptiles, 2 ed., 1923, p. 61; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 67.

Phrynosoma (*Batrachosoma*) *coronatum* Fitzinger, Systema Reptilium, 1843, p. 79.

Phrynosoma cornutum Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, pp. 66-67 (*part.*); Belding, West Amer. Scientist, vol. 3, 1887, p. 98; Stejneger, N. Amer. Fauna, no. 7, 1893, pl. 2 figs. 1a-c.

Phrynosoma asio Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 67; Boulenger, Catalogue of the Lizards in the British Museum (Natural History), vol. 2, 1885, p. 244, (*part.*); Belding, West Amer. Scientist, vol. 3, 1887, p. 98.

Phrynosoma coronatum coronatum Linsdale, Univ. California Publ. Zool., vol. 38, 1932, pp. 367-68; Klauber, Copeia, 1936, pp. 106-110; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 1939, p. 73; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 92; Tevis, Copeia, 1944, pp. 13-18; Smith & Taylor, Univ. Kansas Sci. Bull. vol. 33, pt. 2, 1950, pp. 322, 375; Bull. U. S. Nat. Mus. no. 199, 1950, p. 102.

Taxonomic history: This form first named by de Blainville (1835: 52) from specimens collected by Botta in "California" was thought to occur throughout Baja California. The subsequent naming of new forms from the central and northern parts of the peninsula have restricted *coronatum* to the Cape region.

Diagnosis: This species from the lower part of Baja California can be distinguished by: three or more rows enlarged gular scales on each side; postrictal scale reduced or absent; frontal scales platelike, rugose and light edged.

Description: Head slightly longer than wide; frontal area flattened and covered with large platelike, light-edged scales; superciliary ridges prominent, composed of six unequal scales, the last being the large, triangular superciliary spine; nostrils on, or slightly within, the canthal lines; nostrils separated mesially by one large and two small scales, distance equal to approximately two times diameter of nostril; occipital spines large, grooved and divergent, interoccipital spine prominent; series of enlarged tubercles on occipital shelf at base of occipital spine; temporal shelf moderately developed, bearing four enlarged spines; temporal spines large, increasing in size posteriorly and directed outward (not sloping to the rear); first temporal spine directly below eye, second, third and fourth equally spaced between first and occipital spine; tympanum exposed; labials small, seven in number, infralabials 10-11, in contact with chinshields anteriorly, separated from them posteriorly by one sublabial; chinshields 5-5, increasing in size posteriorly, penultimate largest; subrictal slightly above chinshield row, slightly overlapping fifth chinshield; postrictal small, in line with subrictal; five rows enlarged gular scales of each side of throat; outer row largest;

two lateral neck patches of enlarged spines, lower patch containing largest spines; back covered with small, imbricate, smooth scales interspersed with numerous, large, keeled spines; large spines arranged in three indistinct longitudinal rows on each side, converging into a single paired row on base of tail; two lateral abdominal rows; upper row with much larger spines, extending from above arm insertion to groin; lower row of much smaller spines extending approximately from a point one centimeter behind insertion of arm to a point about one and one-half centimeters in front of insertion of leg; tail with single lateral row; upper and lower leg with several enlarged spines; upper arms bordered anteriorly by two short rows of enlarged scales; ventral abdominal scales smooth, imbricate; postanal area usually with several enlarged scales in males; short series of enlarged spinelike scales lateral to vent; femoral pores 15-17; rows separated mesially by six preanal scales.

Dorsal ground color tan, nuchal blotches reduced to narrow black bands extending from below bases of the occipital spines, (curving caudolaterally) onto shoulder; dorsal blotches reduced to narrow, irregular dark markings; lateral areas darker; frontal area black with narrow reticular light marking on edges of plates; temporal and lateral areas light brown; occipital area mixed black and tan; occipital spines striated; tail with several indistinct slightly darkened bands; venter light tan with few scattered darkened blotches.

Variations: The head usually is longer than wide, being the reverse in only one out of twenty specimens, with three being equally as wide as long. The postrictal scale is completely absent in some specimens but is moderately developed in others. In three specimens from Todos Santos, two have the postrictals only slightly developed, being about one fifth to one fourth the length of the subrictal; in the third the postrictal is much larger being about one half as long as the subrictal. The more northern specimens have a tendency for longer and larger postrictal scales. The subrictal scale varies in position from directly in line with the chinshields to slightly above them. The latter condition is more noticeable in the northern specimens of this subspecies.

The dorsal ground color varies from light gray into medium brown depending upon the substratum. The nuchal blotches may be so large as to cover the major part of the neck area or be reduced to narrow curving bands on the neck and shoulders. The dorsal pattern is generally reduced appearing as narrow irregular bands; however the degree of reduction is not constant.

The femoral pores may be from 14 to 24 on a side with from two to seven preanal scales separating the rows. The ventral scales are smooth with light keeling on those of the chest area.

Discussion: See *P. c. blainvillii.*

General distribution: This form is found in the lower one-fourth of the Peninsula of Baja California, over its entire width.

Locality records: MEXICO. *Baja California:* Cape St. Lucas (USNM 69490, 11538, 11 spec.), (SSNH 17663), (LMK 10778-80, 20521-26), 4 mi. E (LMK 30230); Carnicobra (MVZ 13628); Eureka (MVZ 11741-67); La Paz (USNM 37586-90), 14 mi. SW (17661-62); Medano Armarillo, Magdelina Bay (USNM 13631); Miraflores (AMNH 5499, 5701), (MVZ 13634); Refugio (MVZ 13630), 9 mi. S (LMK 30233); San José del Cabo (KU 2996, 3000), (MVZ 9587, 9779), (SSNH 17664), (USNM 46888, 64465), 15 leagues N (USNM 60401); Santo Domingo (MVZ 13620); Todos Santos (MVZ 11734-39), 7 mi. S (LMK 30232), 15 mi. N (LMK 30231); Triunfo (MVZ 13632); Valle Dares (MVZ 9777); no specific locality (MVZ 13635-36), (USNM 58880).

Phrynosoma coronatum frontale Van Denburgh

Phrynosoma coronata Holbrook, North American Herpetology, 1 ed., vol. 3, 1838, p. 65, pl. 11, and *idem.* 2 ed., vol. 2, 1842, p. 97, pl. 13.

Phrynosoma coronatum Girard, in Stansbury's Expedition to the Valley of the Great Salt Lake of Utah, 1852, p. 36, pl. 7, figs. 7-12; Yarrow & Henshaw, Annual Report to the Chief of Engineers for 1878, Survey West of the 100th Meridian, app. NN. 1878, p. 225; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 70, (*part.*); Gentry, Proc. Acad. Sci. Philadelphia, 1885, p. 143 (*part.*); Townsend, Proc. U. S. Nat. Mus., vol. 10, 1887, p. 238 (*part.*); Fitch, Amer. Midl. Nat., vol. 41, 1949, p. 516.

Tapaya coronata Cooper, Proc. California Acad. Sci., vol. 4 1870, p. 64.

Phrynosoma blainvillei Cope, Bull. U. S. Nat. Mus., no. 1, 1875, p. 49 (*part.*); Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 70 (*part.*); Cope, Report U. S. Nat. Mus. for 1898, (1900), p. 423 (*part.*); Ditmars, The Reptile Book, 1907, p. 152 (*part.*).

Phrynosoma blainvillii Stejneger, N. Amer. Fauna, no. 7, 1893, p. 187, pl. 2, fig. 2.

Phrynosoma frontalis Van Denburgh, Proc. California Acad. Sci., ser. 2, vol. 4, 1894, p. 296.

Phrynosoma frontale Van Denburgh, Occas. Papers California Acad. Sci., no. 5, 1897, p. 93; McLain, Critical Notes on a Collection of Reptiles from the Western Coast of North America, 1899, p. 8; Meek, Field Columbian Mus., Zool. Ser., vol. 7, no. 1, 1906, p. 12; Stone, Proc. Acad. Nat. Sci. Philadelphia, 1911, p. 229; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 1917, p. 59.

Phrynosoma blainvillii frontale Van Denburgh, Occas. Papers California Acad. Sci., no. 5, 1897, p. 95; Bryant, Univ. California Publ. Zool., vol. 9, 1911, pp. 5, 38, pl. 5; Van Denburgh, Proc. California Acad. Sci., ser. 4, vol. 3, 1912, p. 148; Grinnell & Camp, Univ. California Publ. Zool., vol. 17, 1917, p. 165; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, vol. 1, 1922, pp. 385-401, pl. 33; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 2 ed. 1923, p. 60; Burt, Jour. Washington Acad.

Sci., vol. 19, 1929, pp. 453-454; Bogert, Bull. So. California Acad. Sci., vol. 29, 1930, p. 7; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 66; Klauber, Copeia, 1936, pp. 103-110 (*part.*); Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed., 1939, p. 72; Cowles, Science, NS, vol. 90, 1939, pp. 465-466; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 91 (*part.*).

Phrynosoma coronatum frontale Linsdale, Univ. California Publ. Zool., vol. 38, 1932, p. 367; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, pp. 356, 375; Bull. U. S. Nat. Mus. no. 199, 1950, p. 103.

Taxonomic history: Van Denburgh (1894) recognized the distinctiveness of this form and described it as a full species from a specimen in the Stanford University Collection taken by Gilbert and Price in Bear Valley San Benito County, California. Van Denburgh later (1897) found specimens that appeared to show intergradation with *blainvillii* and suggested that if this were the case, it should be given subspecific rank under *blainvillii*. Bryant (1911) adequately demonstrated the intergradation.

Diagnosis: Three or more rows enlarged gular scales on each side; postrictal spine large; five closely set temporal spines gradually increasing in size posteriorly; frontal scales small, often pointed and rugose.

Description: Head broader than long; frontal area slightly concave, covered with small, often pointed, rugose scales; superciliary ridge not prominent; nostrils on canthal line; internasal distance equal to three and one-half or four times nostril diameter; occipital shelf with four enlarged erect tubercles; occipital spines long, separated mesially by a distance equal to basal diameter; interoccipital spine moderately large; temporal shelf moderately expanded, bearing five enlarged pointed spines; temporal spines closely set, curved posteriorly, largest subequal to occipital spine; supralabials small, inconspicuous; infralabials small, in contact with chinshields anteriorly separated posteriorly by three minute sublabials; chinshields increasing in size posteriorly; subrictal completely above line of chinshields; postrictal long and slender, on line of chinshields; three rows of enlarged gular scales on each side; two lateral neck patches, lower one most prominent; dorsal scales minute, smooth, imbricate; numerous large keeled scales dispersed over back; two rows of enlarged, spinelike scales in lateral abdominal fringe, upper row largest and most extensive; vertebral line covered with medium, imbricate, keeled scales; several indistinct rows of spines on tail; ventral scales small, imbricate and smooth; femoral pores 14-14 with four preanal scales separating the rows mesially.

Dorsal ground color gray; nuchal blotches dark brown to black; dorsal pattern of three pairs of irregular bars edged posteriorly in light buff; tail with several indistinct transverse bars; head olive; frontal scales stippled with brown; ventral scales cream with numerous irregular dark brown bars.

Variation: The width of the head is equal to, or exceeds, its length by as much as 17 percent in all but two of the specimens measured in this study. The fourth temporal spine (counting from rear forward) may be reduced in size or entirely absent.

Discussion: See *P. c. blainvillii.*

Distribution: Central California west of the Sierra Nevadas, south into southern Ventura, northern Los Angeles, and western San Bernardino counties.

Locality records: CALIFORNIA. *Alameda Co.*: Berkeley (MVZ 2291, 11030, 12734, 17147, 17985); 7 mi. SE (MVZ 38945, 38976); Livermore 9 mi. SE (MVZ 36298). *Calaveras Co.*: Mokelumne Hill (Van Denburgh, 1922). *Contra Costa Co.*: Antioch (MVZ 43826-27); Brentwood (MVZ 12263); Mt. Diablo (MVZ 24126), west side of (MVZ 3954), Castle Rock Park (MVZ 33623); Rock City (MVZ 33627); Skeleton Tree (MVZ 33626). *El Dorado Co.*: Placerville (Van Denburgh, 1922); no specific locality (USNM 160). *Fresno Co.*: Fresno (USNM 11760,, 11793, 12568, 18453-55, 45137); Mendota (USNM 34613-14, 34616-20). *Kern Co.*: Asphalto (Van Denburgh, 1922); Bakersfield (USNM 18456), west of (SSNH 11176); Bodfish (Van Denburgh, 1922); Brechenridge (Van Denburgh, 1922); Button Willow (Van Denburgh, 1922); Canada de los Uvas (USNM 18460); Carrizo Plains (USNM 18457-58); Chimney Rock (Van Denburgh, 1922); Cuddy Valley (LMK 2850); Dow (LMK 2715-16); Fort Tejon (USNM 4587, 10 spec., 4588, 10 spec., 18459, 32335); Kern River, S. Fork (USNM 10784, 16440, 18450); Kern Valley (Van Denburgh, 1922); Kernville (USNM 18451-52); Maricopa (LMK 8810); McKittrick, 3 mi. N (SSNH 16052); Ft. Pinos (LMK 5182-84); Onyx (Van Denburgh, 1922); Rose Station (Van Denburgh, 1922); San Emidio Plains (Van Denburgh, 1922); Tehachapi Mountains (Van Denburgh, 1922); Walker Basin (USNM 18449); Walker Pass (USNM 18446-48); Weldon (Van Denburgh, 1922); Wheeler Ridge Road (Van Denburgh, 1922). *Kings Co.*: Lemoore (Van Denburgh, 1922). *Los Angeles Co.*: Alhambra (USNM 17404-07); Antelope Valley, Elizabeth Lake (Van Denburgh, 1922); Burbank (USNM 45135); Mescal Gulch (LMK 2720); Neenach, 5 mi. S (Grinnell

& Camp, 1917); Placerita Cañon (USNM 54842), (LMK 4370-71); San Francesquito Canyon (LMK 2717); Tujunga Canyon (Grinnell & Camp, 1917); Tujungan Wash (LMK 2719); no specific locality (USNM 13949, 2 spec.). *Madera Co.*: Madera (MVZ 42710), 5 mi. S (Van Denburgh, 1922); San Joaquin Experiment Range (Fitch, 1949). *Mariposa Co.*: Coulterville, 5 mi. NE (Grinnell & Camp, 1917). *Merced Co.*: Caldwell (USNM 5433); Gadwall (Van Denburgh, 1922); Livingstone (LMK 38173-74), (Stanford 3614), 4-5 mi. W (LMK 38079-80); Los Banos, 22 mi. S (USNM 2541, 2543-44), (Stanford 3697). *Monterey Co.*: Abbot's Ranch (Van Denburgh, 1922); Arroyo Seco (Van Denburgh, 1922); Carmel, 9 mi. E (MVZ 38616), Valley (Stanford 3325); Del Monte (MVZ 9321), (USNM 44603-04); King City (SSNH 11175), 9 mi. NE (LMK 27528), 24 mi. W (AMNH 37218); Metz (Van Denburgh, 1922); Monterey (USNM 156, 7908); Nottley's Landing, 10 mi. E (MVZ 16699-700); Pacific Grove (Van Denburgh, 1922); Sea Side (USNM 44601-02); Soledad, 5½ mi. ENE (MVZ 39075-76); Tassajara Creek (USNM 46809-10); Watsonville, 7 mi. S (MVZ 6327-28). *Placer Co.*: Auburn (Van Denburgh, 1922); Forest Hill (Van Denburgh, 1922); *Sacramento Co.*: American River, near Folsom (LMK 25836); Fair Oaks (LMK 25835); Roseville (LMK 27329); Sacramento (LMK 25834, 27294-95). *San Benito Co.*: Bear Valley (Stanford Mus. 93 type); Hernandez, 4 mi. S (MVZ 21355); Pinnicales Post Office, 4 mi. NW (MVZ 36189), 4 mi. W (MVZ 36190); San Benito (MVZ 21356); San Juan (Van Denburgh, 1922). *San Francisco Co.*: San Francisco (USNM 8862). *San Joaquin Co.*: Alameda Co. line, ½ mi. E (MVZ 33701); Lathrop (MVZ 3551-52, 3555, 3568-69, 3572, 3797, 4799, 4803); Ripon (MVZ 7188), (Stanford 3327); Stockton (LMK 25999); Tracy (Grinnell & Camp, 1912). *San Luis Obispo Co.*: Edna (Van Denburgh, 1922); San Juan River, S of Shandon (Van Denburgh, 1922); Shandon (Van Denburgh, 1922); Simmler, 5 mi. S (SSNH 16038-44); Temblor Mountain (Van Denburgh, 1922). *San Mateo Co.*: Searsville, (Van Denburgh, 1897). *Santa Barbara Co.*: Big Pine (MVZ 34627); Bluff Camp (MVZ 35292, 35339-41); Cuyama Valley (USNM 48729, 59839-42); San Marcos Grade, Summit (LMK 20765-66); Santa Barbara (USNM 8648, 10780), 8 mi. NE (MVZ 35291, 35342-43, 43626), (LMK 37710, 38688). *Santa Clara Co.*: Canada Valley (Van Denburgh, 1897); Congress Springs (Van Denburgh, 1922); Coyote Creek (Van Denburgh 1897); Gilroy (Van Denburgh, 1922); Livermore, 40 mi. SE (MVZ 36425); Los Gatos (Van Denburgh, 1922); Lyndon

(Van Denburgh, 1922); Mayfield (Van Denburgh, 1897); Morganhill (Van Denburgh, 1897); Mt. Hamilton (USNM 53599); Mountain View (Van Denburgh, 1922); Santa Clara (Van Denburgh, 1897); Smith Creek (Stanford 3324); Stanford (Van Denburgh, 1922); Wrights (Van Denburgh, 1897). *Santa Cruz Co.*: Watsonville (Van Denburgh, 1922). *Shasta Co.*: Kenneth (LMK 25837). *Sonoma Co.*: Bodega (USNM 154). *Tulare Co.*: Earlimart (Van Denburgh, 1922); Goshen (Van Denburgh, 1922); Pixley (LMK 23971); Tipton (USNM 45136); Tulare Lake, W side (USNM 44807); Visalia (LMK 20924). *Ventura Co.*: Lockwood Valley (LMK 2718); Matilija (Van Denburgh, 1922); Mount Pinos (Van Denburgh, 1922); Montalva (Van Denburgh, 1922); Nordhoff (Van Denburgh, 1922); Sespe Creek (AMNH 44340, 44361).

Phrynosoma coronatum jamesi Schmidt

Phrynosoma jamesi Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 46, 1922, pp. 668-669, pls. 55, 56; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 2 ed., 1923, p. 62; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 68.

Phrynosoma coronatum jamesi Linsdale, Univ. California Publ. Zool., vol. 38, 1932, pp. 349, 369; Klauber, Copeia, no. 2, 1936, pp. 103-110; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed., 1939, p. 73; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 93; Tevis, Copeia, no. 1, 1944, pp. 13-18; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, pp. 321, 375; Bull. U. S. Nat. Mus., no. 199, pp. 102-103.

Taxonomic history: This form of central Baja California was named by Schmidt (1922:668) from a specimen collected at San Bartolomé Bay by H. Townsend. It was reduced to subspecific status by Linsdale (1932) where it has since remained.

Diagnosis: Three or more rows of enlarged gular scales on each side of throat; four enlarged temporal spines on each side of head, fourth from rear reduced leaving a gap in the continuity; postrictal present and moderately developed; subrictal slightly above the row of chinshields; five chinshields on each side.

Description: Head slightly longer than wide; frontal area flattened, covered with dark platelike scales bordered in light color; nostrils large, on the canthal line; occipital horns large, slightly divergent; interoccipital spine moderately developed; four temporal spines on each side; bases of two center temporal spines in contact; temporal shelf slightly developed; occipital shelf with several enlarged tubercular scales; superciliary ridge inconspicuous, terminating posteriorly in slightly enlarged triangular spine; tympanum exposed; labials small, inconspicuous; infralabials small, in contact

with chinshields; chinshields five on each side, increasing in size posteriorly; subrictal slightly above level of chinshields; postrictal scale moderately long and thin; four rows or enlarged gular scales on each side; two lateral neck patches; back covered with small, imbricate, smooth scales interspersed with enlarged, keeled scales; enlarged scales forming three pair of indistinct longitudinal rows; rows converging on tail base to a single pair; two rows enlarged lateral spines, lower pair greatly reduced; ventral scales smooth; femoral pores 17-17, rows separated mesially by four preanal scales.

Dorsal ground color grayish; nuchal blotches distinct; dorsal blotches reduced to narrow irregular bands; bands edged posteriorly in lighter color; several indistinct dark bands on tail; frontal area dark; light scale edges forming reticulate pattern; temporal and lateral areas tan; ventral area light with few scattered dark spots.

Variation: The size and pattern of the frontal scales varies from the large, dark scales prevalent in *coronatum* to a much reduced, slightly rugose scale approaching the condition found in *schmidti.* The postrictal is always present but varies in size and distinctness. In the above two characters the trend is, in general geographically consistent, changing gradually from south to north. The temporal spines vary in number and arrangement. Four is the usual number; however, a fifth may appear between the third and fourth becoming, in some specimens, larger than the fourth. The spines may project laterally or be angled posteriorly. From 14 to 20 femoral pores are present with from one to seven preanal scales separating the rows mesially.

Discussion: Specimens from Barril and San Francisquito Bay appear distinct and may be found to be a new form when others are available.

General distribution: Central part of Baja California approximately between the latitudes of 26°20′ and 28°40′.

Locality records: Mexico: *Baja California:* Abreojos Pt. (LMK 38927, 40077-78), 35 mi. E (LMK 38945); Ballenas Bay (LMK 38939); Barril (SSNH 18082-84); Calmalli, 3 mi. W (MVZ 13625); El Arco (SSNH 18087), 14 mi. SE (MVZ 37333); Loreto (LMK 30234, 30236-41); Los Ángeles Bay (LMK 39003); Miller's Landing, 1 mi. SSE (MVZ 37331), 5 mi. ESE (MVZ 37332); Mulege (Van Denburgh, 1922); San Augustin, 2 mi. E (SSNH 18091); San Bartolmé Bay (USNM 64450), (AMNH 5497); San Francisquito Bay (SSNH 18085); San Ignacio (MVZ 10659-60, 13637-40), 20 mi. N

(MVZ 13626-27); Santa Rosalia (Van Denburgh, 1922); Punta San Jacinto, plains north of (SSNH 18520); between and Punta Camalu (SSNH 18517).

Phrynosoma coronatum schmidti Barbour

Phrynosoma coronatum Meek, (*nec.* Blainville), Field Columbian Mus., Publ. Zool. vol. 7, 1905, p. 12; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, vol. 1, 1922, pp. 403-406 (*part.*).

Phrynosoma schmidti Barbour, Proc. New England Zool. Club., vol. 7, 1921, p. 113; Stejneger and Barbour, Check List of North American Amphibians and Reptiles, 2 ed., 1923, p. 63, 3 ed., 1933, p. 69 and 4 ed., 1939, p. 75, and Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 95.

Phrynosoma nelsoni Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 46, 1922, pp. 666-668, pl. 54, fig. 3; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 2 ed., 1923, p. 63; Stejneger & Barbour, *idem*, 3 ed., 1933, p. 69.

Phrynosoma coronatum blainvillii Linsdale, Univ. California Publ. Zool., vol. 38, 1932, pp. 349, 368 (*part.*).

Phrynosoma ochoterenai Cuesta Terron, Anal. Inst. Biol., vol. 3, 1932, p. 109.

Phrynosoma blainvillii frontale Klauber, Copeia, 1936, pp. 103-110 (*part.*); Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 91 (*part.*); Tevis, Copeia, 1944, pp. 13-18; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, 1950, pp. 323, 375; Bull. U. S. Nat. Mus., no. 199, 1950, p. 103.

Diagnosis: Three rows enlarged gular scales on each side; three posterior temporal spines, significantly enlarged, and directed laterally; head slightly longer than wide; frontal scales small, pointed, rugose, without dark pigment; subrictal scale distinctly above row of chinshields.

Description: Head slightly longer than wide; frontal area flat, covered by small, rugose scales; rostrofrontal angle obtuse; nostrils above canthal line, separated by distance equal to three times diameter of one nostril; superciliary ridge distinct, terminating posteriorly in blunt triangular spine; occipital shelf bearing four medium-sized tubercles; interoccipital spine small; occipital spines well developed; interoccipital distance equal to basal diameter of one spine; temporal area moderately developed, bearing five enlarged laterally projecting spines; three posterior showing marked enlargement; supralabials and infralabials inconspicuous; chinshields in contact with infralabials throughout; subrictal scale distinctly above row of chinshields; postrictal of medium size; three enlarged rows of gular scales on each side; tympanum exposed; dorsal scales small, imbricate, smooth; eight indistinct longitudinal rows of enlarged, keeled scales, four of which continue onto base of tail; two rows of enlarged flexible spines in lateral abdominal fringe, upper row largest; two short rows of enlarged scales on femur; two rows of enlarged, pointed, imbricate, keeled scales on humerus; ventral scales

smooth throughout; femoral pores 16-17, rows separated mesially by five preanal scales.

Dorsal ground color light gray, nuchal spots dark brown; four equally spaced, incomplete, irregular, dark brown bars between nuchal spots and rump; tail with six transverse bars; head olive; larger spines with dark striations; ventral scales cream with reticulate black markings.

Variation: The frontal scales vary from the small, convex rugose condition found on the specimens from near San Quintín to larger, smoother condition northward, intergrading with *blainvillii* and southward becoming larger, flatter and darker. The temporal spines are distinct from each other in *schmidti,* giving the head a more jagged appearance. The fourth spine is typically reduced and is often found in a position slightly above the remaining row in which case the bases of the third and fifth scales may be in contact. However, specimens can be found in the northern localities that has this spine in place in the row and of expected size.

The ground color, as expected changes with the substratum and may vary from ivory, through the tans and browns to a dull gray. The pattern is generally distinguishable and may vary in color from brown to black. A few dark flecks may be found on the frontal scales in the more southern specimen.

Discussion: The name *Phrynosoma schmidti* Barbour antedates *Phrynosoma nelsoni* Schmidt and therefore must be used if the specimens from Cedros Island are to be included in this subspecies. The specimen from Punta Prieta and vicinity approach an intermediate stage between *schmidti* and *jamesi.* However, the majority of their characters seem to be slightly nearer those of the typical *schmidti,* thus justifying their placement here.

General distribution: This subspecies ranges generally between Lat. 28°50′ to near 31°50′. The northern distribution is confined to the area west of the Sierra Juarez and the Sierra San Pedro Mártir.

Locality records: Mexico. *Baja California:* Aguajeta, 10 mi. S (SSNH 16719), 15 mi. S (SSNH 16720); Arroyo Medano Crossing (between Arroyo San Miguel Lat. 31° 51′ and Pt. Descanso Lat. 32°15′), 4 mi. N (LMK 38380); Catavina Lat. 29°49′, 19 mi. N (LMK 40411-12); El Marmol Lat. 29°37′ (LMK 39216); Ensenda Lat. 31°52′, 17 mi. N (LMK 40415); Hamilton Ranch, somewhere between Lats. 30°30′ and 31°30′ (LMK 39036), 10 mi. N (LMK 38944), 37 mi. S (SSNH 16718), 43 mi. S (SSNH 16716-17); La Grulla Lat. 30°56′ San Pedro Mártir Mountains 10 mi. W (LMK

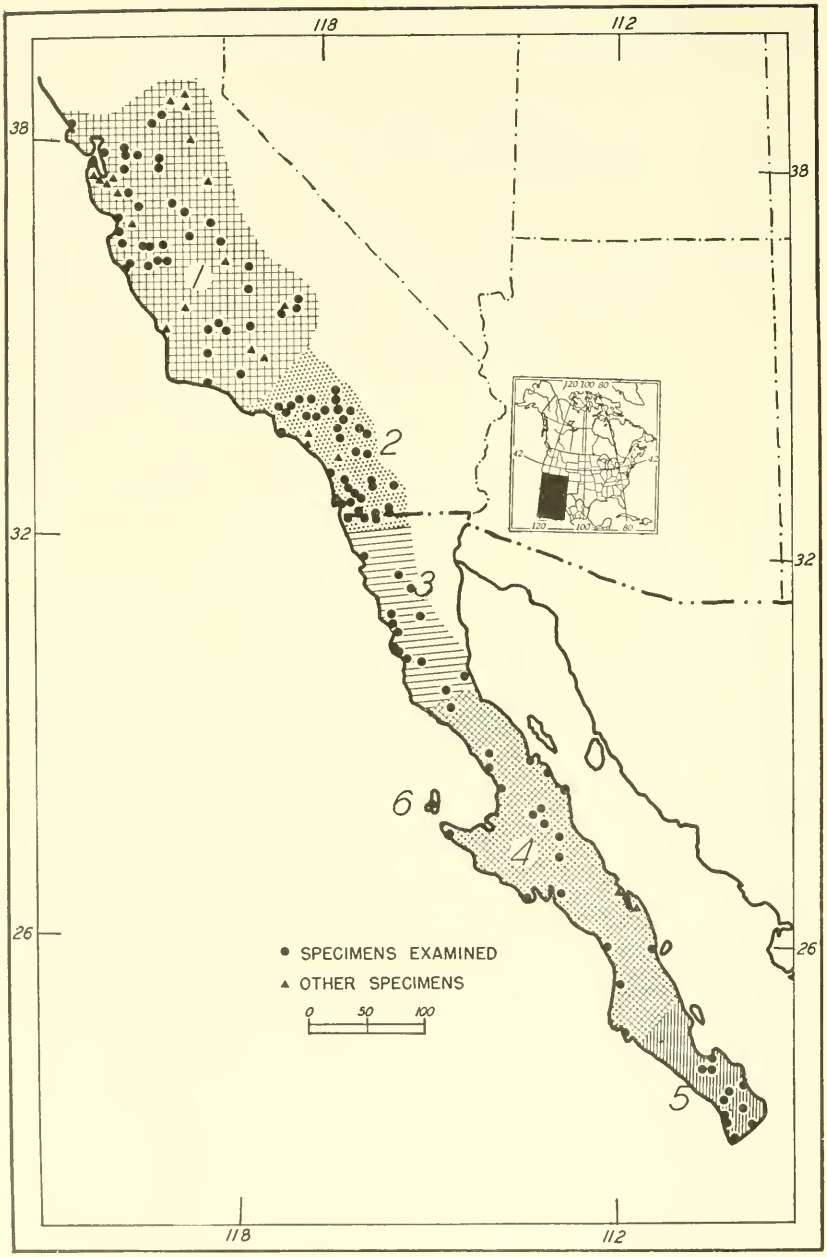

FIG. 5. Map showing the geographic distribution of the coronatum group.

1. *Phrynosoma c. frontale*
2. *Phrynosoma c. blainvillii*
3. *Phrynosoma c. schmidti*
4. *Phrynosoma c. jamesi*
5. *Phrynosoma c. coronatum*
6. *Phrynosoma cerroense*

2722-24); Loreto, Mission San Fernando, near Lat. 30°, 6 mi. E (LMK 40414); Punta Prieta, Lat. 28°58′ (SSNH 16705), 2 mi. NW (MVZ 37329), 10 mi. S (SSNH 18088), 18 mi. S (SSNH 18089); Punta San Jacinto, Lat. 30°52′, opposite (LMK 39656), base of (LMK 40024); Río San Rafael Valley, Lat. 31°50′ (LMK 40164); Rosario, 30°50′ 5 mi. E (MVZ 37326), 20 mi. E, 2 mi. S (MVZ 37327), 25 mi. E (LMK 38332), 30 mi. E (MVZ 37328), 36 mi. E (LMK 40409-10); San Antonio, Lat. 30°20′, 1 mi. N (SSNH 16707); San José, Lat. 31° (LMK 4576-89, 8822); San Quintin, Lat. 30°38′ (USNM 37585), (LMK 20160, 32618), (MVZ 37323), plains of (LMK 39364), 3 mi. E (SSNH 18080); 7 mi. NNW (MVZ 37321-22), 8 mi. SE (MVZ 37324); San Telmo (MVZ 9778); Santo Tomás Canyon, Lat. 31°34′ (LMK 39770), between Hamilton Ranch and (SSNH 16703-04); Socorro, Lat. 30°20′ (LMK 32129-30), 2 mi. SSE (MVZ 37325); Santa Domingo, Lat. 30°45′ (MVZ 37320), 18 mi. NW (MVZ 37319); Valle Trinidad (LMK 20038).

Cedros Island (AMNH 20583).

Phrynosoma cerroense Stejneger

Phrynosoma Belding, Proc. U. S. Nat. Mus., vol. 5, 1883, p. 530.

Phrynosoma hernandezi Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 68 (*part.*); Belding, West Amer. Scientist, vol. 3, no. 24, 1887, p. 99.

Phrynosoma cerroense Stejneger, N. Amer. Fauna, no. 7, 1893, p. 187; Van Denburgh, Proc. California Acad. Sci., ser. 2, vol. 5, 1895, p. 199; Cope, Report U. S. Nat. Mus. for 1898 (1900), p. 428, fig. 75; Van Denburgh, Proc. California Acad. Sci., ser. 3, vol. 4, no. 1, 1905, pp. 3, 23; Ditmars, Reptiles of the World, 1910, p. 151; Ditmars, Reptile Book, 1907, p. 151; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, 1914, pp. 132, 144; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 1917, p. 58; Nelson, Mem. Nat. Acad. Sci., vol. 16, 1922, pp. 114, 130; Schmidt, Bull. Amer. Mus. Nat. Hist. vol. 16, 1922, pp. 607-707; Van Denburgh, Occas. Papers California Acad. Sci. 1922, pp. 401-403; Stejneger & Barbour, Check List North American Amphibians and Reptiles, 1923, pp. 60-61; Cuesta Terron, Inst. Biol. Univ. Nat. Mus., 1932, p. 109; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 66; Klauber, Copeia, no. 2, 1936, pp. 103-110; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed., 1939, p. 72; Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 92.

Phrynosoma coronatum cerroense Linsdale, Univ. California Publ. Zool. vol., 38, no. 6, 1932, p. 368.

Diagnosis: Three rows of enlarged gular scales on each side; frontal scales of medium size, rugose and colored dark brown or black; four temporal spines on each side, fourth from rear, missing in adults, much reduced in young; subrictal in line with chinshields, postrictal present; chinshields usually reduced to four on each side.

Description: Head slightly longer than wide; frontal area flat, covered with medium sized, rugose scales; rostrofrontal angle obtuse; nares small, separated by distance equal to one and one-half

times diameter of one naris, nares within the canthal lines; supralabials and infralabials inconspicuous; chinshields, reduced to four on each side, in contact with infralabials; subrictal in line with chinshields; postrictal of medium size, cone shaped; three rows enlarged gular scales on each side; two neck patches enlarged lateral scales, upper patch only slightly enlarged; tympanum exposed; occipital shelf bearing four tubercles; occipital spines of medium size, interoccipital space equal to basal diameter of single spine; interoccipital spine small; four enlarged temporal spines, increasing in size posteriorly; superciliary ridge terminating posteriorly in short, blunt, triangular spine; dorsal scales small, imbricate, smooth; eight longitudinal rows of enlarged keeled scales between neck and rump; four rows continuing on rump and base of tail, converging into two rows on tail; two rows of enlarged flexible spines in lateral abdominal fringe, lower row markedly reduced; ventral abdominal scales small, smooth; femoral pores 17-18, rows separated mesially by two preanal scales.

Dorsal ground color steel-gray; dark nuchal spots distinct dorsally, fading ventrolaterally into ground color; three pair of equally spaced, irregular, dark gray to black blotches on remainder of back; tail with five indistinct, dark transverse bars; head olive; frontal scales dark brown to black; spines medium brown; ventral scales cream with numerous black spots.

Variation: Of the four specimens of this species available in this study three were fully adult and one a juvenile. In the adults the temporal spine that would normally, in *frontale* and *blainvillii*, be considered the fourth, is in *cerroense* reduced to a small scale at the base of the third, leaving the impression that only four spines are present. In the juvenal specimen this fourth spine was present in its proper place but was much reduced.

The frontal scales are of equivalent size, and texture in all the specimens, however, the dark coloring was less intense on the juvenile. The ground color varies from the steel-gray of the adults to a light brown in the juvenile. The pattern is more clearly distinguishable in the young specimen.

Discussion: While at the United States National Museum, I had an opportunity to compare the type specimens of *cerroense* and *jamesi*. The two specimens are of nearly equivalent size and both are in very good condition. The comparison demonstrated a great similarity in the two; so much so that no more than subspecific status would be considered if both were mainland forms. Their measure-

ments and proportions coincide closely, the color and color patterns were generally the same, the general scalation was the same (including a second lateral abdominal row, supposedly absent in *cerroense*) and in general the two appear to differ but little. However, at least one character seemed to separate the two. The five chinshields and the subrictal form in *jamesi*, the enlarged row of serrate scales along the lower jaw. This same series in *cerroense* was composed only four chinshields, the subrictal with a larger gap between the last chinshield, and the subrictal, compensating for the missing scale. Additional material appears to validate this difference, although a total of five specimens of *cerroense* is all that was available for this study.

The complete isolation of *cerroense* rather than the minor anatomical variations has, I believe, led to its designation as a full species. This appears to be in keeping with the general trend of taxonomists in handling insular forms, and undoubtedly is the best procedure in this particular case. A second form (*schmidti*) has been described from the island, and from my observations of the paratype at the American Museum of Natural History, it appears to be distinctly different from *cerroense* and very close to, if not identical with, specimens from northern Baja California here referred to as *P. c. schmidti*. The occurence of the two forms on the same island would seem to indicate that they were either variants of the same subspecies, as some believe to be the case, or that they are species distinct one from the other. I incline to the view that *cerroense* has reached full specific status and that *schmidti* is a subspecific form identical with the mainland form heretofore considered as the southern population of *frontale*. Collecting of additional specimens and a careful ecological study of their relationships on the island are needed before the true status of the forms will be known.

General distribution: This species is confined to Cedros Island.

Locality records: Mexico. *Baja California:* Cedros Island. SW side (SSNH 17369), village, 3 mi. S (SSNH 17370), no specific locality (LMK 24357), (USNM 11977).

Phrynosoma asio Cope

Phrynosoma asio Cope, Proc. Acad. Nat. Sci. Philadelphia, vol. 16, 1864, pp. 178-179; Günther, Biologia Centrali-Americana, Reptilia and Batrachia, 1890, p. 79; Cope, Rept. U. S. Nat. Mus., 1898 (1900), pp. 407-408; Gadow, Proc. Zool. Soc. London, 1905, pp. 194, 213; Ditmars, Reptiles of the World, 1910, p. 151; Smith, Trans. Kansas Acad. Sci., vol. 37, 1934, pp. 287-288; Oliver, Occas. Papers Mus. Zool. Univ. Michigan, no. 360,

1937, p. 10; Hartweg & Oliver, Misc. Publ. Mus. Zool. Univ. Michigan, no. 47, 1940, p. 16; Smith, Ann. Carnegie Mus., vol. 30, 1944, p. 89; Smith & Laufe, Trans. Kansas Acad. Sci., vol. 48, 1945, p. 337; Schmidt & Shannon, Fieldiana Zool., vol. 31, 1947, p. 74; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 3, pt. 2, 1950, p. 328; Smith & Taylor, Bull. U. S. Nat. Mus., no. 199, 1950, p. 102.

Phrynosoma spinimentum, Peters, Monatsb. Akad. Wiss. Berlin, 1873, pp. 742-743.

Batrachosoma asio Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 4, 1874, pp. 241-242, pl. 17, figs. 9a-e.

Taxonomic history: Cope (1864:178) named this species from specimens in the United States National Museum collected by John Xantus in Colima, Mexico. Bocourt (1874) placed it in his subgenus *Batrachosoma.* Cope (1900) placed the species in the genus *Phrynosoma.*

Peters (1873:742-743) described *P. spinimentum* as a new species from a specimen taken in Tehuantepec, Mexico. This is undoubtedly a specimen of *P. asio.*

Diagnosis: Nostrils on canthal line; two peripheral rows of abdominal spines; three or four series of gular scales; ventral abdominal scales keeled throughout.

Description: Head equally as broad as long; nostrils on canthal line, separated by two small scales; superciliary ridges distinct, edged with four or five elongated scales, terminating posteriorly in large sharp spine; frontal scales subequal; occipital horns smaller than largest temporal, directed from skull at angle of approximately 90°; two diverging temporal spines; tympanum large and exposed; infralabials and chinshields separated by maximum of three small sublabials; gular scales irregular in size, with three or four enlarged rows on each side; gular fold bearing patch on each side containing four enlarged pyramidal scales; lower of two neck patches in line with chinshields, upper in line with lateral abdominal fringe; neck patches of single lone spines set in rosette of smaller scales. Back covered with small imbricate scales interspersed with varying sizes of enlarged keeled scales; eight distinct longitudinal rows of enlarged, keeled scales between neck and rump; above rows converging into four on rump and base of tail; two rows on tail; short medium nuchal row of spines present; two rows of enlarged soft spines in lateral abdominal fringe; femur and tibia with two rows of spines; arms bearing several rows of strongly-keeled scales; ventral scales keeled throughout, less definitely so posteriorly; about thirty-five scales across widest part of abdomen; femoral pores eight to nine on a side, with 18 to 20 preanal scales separating the two rows.

Dorsal ground color ashy gray with pair of distinct dark-brown

neck blotches extending posteriorly outside largest row of spines; color becoming fainter posteriorly; four incomplete transverse, light-bordered bands in front of rump; bands may appear as alternating spots; tail bearing variable number of transverse bands. Ventral scales cream, without dark spots.

Variation: The ground color varies from a medium brown to a light gray. The pattern may be somewhat obscured by fading of the colors, but is generally discernible. In the young the pattern may or may not be apparent; the ventral scales are generally more heavily keeled and may carry a considerable amount of dark pigment, which is generally in spots.

Discussion: Individuals of this species probably reach the largest size found in the genus. The largest specimen measured in this study was the type (USNM 32216) from Colima, Mexico, which has a snout-vent measurement of 115 mm. and a total length of 202 mm. (approx. 8 inches). Twelve of thirty one specimens exceeded 100 mm. in snout-vent measurement.

The occurrence of this species in Guatemala represents the most southern locality recorded for any member of the genus. The type locality has been restricted to Colima city, Colima, Mexico, by Smith & Taylor (1950a).

Locality records: Mexico. *Colima:* Colima (city) (USNM 32216, 217); Tecomán (Smith, 1944). *Michoacán:* Apatzingán (Schmidt & Shannon, 1947); Copradice (Smith & Taylor, 1950b); La Salada (USNM 47739); San Salvador (Smith & Taylor, 1950b). *Guerrero:* Mezcala (on Río Balsas). *Oaxaca:* Escurana (USNM 111358-63), (AMNH 66919); Ranchero Poso Río (Hartweg & Oliver, 1940); Salina Cruz (AMNH 18477-81, 18483, 62320); San Genoino (USNM 47056-57); San Pedro (Hartweg & Oliver, 1940); Tehuantepec (USNM 30476-79, 113275, 11357), (AMNH 18476, 58627-38, 58060-61, 65815-18, 66922-25); 1 mi. N (AMNH 62607). *Chiapas:* no specific locality (Smith & Taylor, 1950b).

Central America. *Guatemala:* Savana Grande (Günther, 1890).

Phrynosoma cornutum (Harlan)

Agama cornuta Harlan, Journ. Acad. Nat. Sci. Philadelphia, vol. 4, 1825, p. 299, pl. 20; Harlan, Medical and Physical Researches, 1835, p. 141.

Phrynosoma bufonium Wiegmann, Isis von Oken, vol. 21, 1828, p. 367; Gray, in Griffiths Cuvier's Animal Kingdom; Syn. Rept., 1831, p. 45.

Tapaya cornuta Cuvier, Règne Animal, vol. 2, 1829, p. 37.

Phrynosoma cornutum Gray, *in* Griffiths, Cuvier's Animal Kingdom; Syn. Rept., 1831, p. 45; Holbrook, North American Herpetology, 1 ed. vol. 3, 1838, p. 55, pl. 9, and *idem*, 2 ed. vol. 2, 1842, p. 87, pl. 11; Dekay, Zoology of New York, vol. 3, 1842, p. 31; Gray, Catalogue of the Lizards in the

British Museum of Natural History, 1845, p. 229; Girard, *in* Stansbury's Exploration of the Valley of the Great Salt Lake of Utah, 1852, p. 360, pl. 8, figs. 1-6; Hallowell, Sitgreaves' Expedition down the Zuni and Colorado Rivers, 1853, pp. 119, 145; Baird & Girard, Proc. Acad. Nat. Sci. Philadelphia, vol. 6, 1853, p. 301; Baird & Girard, *in* Marcy's Exploration of the Red Rivers, 1854, p. 204; Hallowell, Proc. Acad. Sci. Philadelphia, vol. 8, 1856, p. 239; Girard, Exploring and Expeditions of Years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, USN, vol. 20, 1858, Herpetology, p. 403, pl. 21, figs. 6-9; Baird, United

FIG. 6. Map showing the geographic distribution of the species *Phrynosoma asio*.

States Mexican Boundary Survey under the order of Lieut. Col. W. H. Emory, Reptiles of the Boundary, vol. 2, 1859, p. 9; Baird, Report of the Pacific Rail Road Survey, vol. 10, 1859, p. 37; Aug. Duméril & Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 1, 1870, pl. 12, fig. 9; Bocourt, *idem*, livr. 4, 1874, pp. 236-238, pl. 12, figs. 9-9b; Cope, Proc. Amer. Philos, Soc., vol. 18, 1870, p. 261; Cope, Bull. U. S. Nat. Mus., no. 1, 1875, p. 49; Yarrow, Report of the Geography and Geology of the Survey West of the 100th Meridian, under Lt. Wheeler, vol. 5, 1875, p. 579 (*part.*); Yarrow & Henshaw, Report of the Chief of Engineers for Survey West of the 100th Meridian App. NN, 1878, p. 226 (*part.*); Müller, Verh. Nat. Gesell., Basel, 1878, p. 634; Cope, Proc. Amer. Philos. Soc., 1879, p. 261; Hoffman, Amer. Nat., vol. 13, 1879, pp. 326-327; Boettger, Zool. Garten, 1879, pp. 289-293; Cope, Bull. U. S. Nat. Mus., no. 17, 1880, pp. 17, 44, 46; Cragin, Trans. Kansas Acad. Sci., vol. 7, 1881, p. 114; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, pp. 11, 66 (*part.*); Cope, Proc. Acad. Nat. Sci. Philadelphia, vol. 35, 1883, pp. 10, 12; Lockwood, Amer. Nat., vol. 17, 1883, pp. 682-683; Cragin, Bull. Washburn Lab. vol. 1, 1884, p. 7; Nehring, Zool. Garten, vol. 25, 1884, pp. 230-234, 259-262; Garman, Bull. Essex Inst. vol. 16, 1884, p. 19; Boulenger, Catalogue of the Lizards in the British Museum Natural History, vol. 2, 1885, pp. 245-246; Gentry, Proc. Acad. Nat. Sci. Philadelphia, vol. 22, 1885, p. 145; Schufeldt, Science, vol. 6, 1885, pp. 185-186; Cope, Proc. Amer. Philos, Soc. vol. 23, pt. 2, 1886, pp. 169, 282; Cope, Bull. U. S. Nat. Mus., no. 32, 1887, p. 398; Garman, Bull. Essex Inst., vol. 19, 1887, p. 13; Belding, West Amer. Sci., vol. 3, 1887, p. 98; Cope, Proc. U. S. Nat. Mus., vol. 11, 1888, p. 398; Günther, Biologia Centrali-Americana, Reptilia and Batrachia, 1890, p. 79; Cope, Proc. Acad. Nat. Sci. Philadelphia, vol. 29, 1892, p. 335; Van Denburgh, Proc. California Acad. Sci., ser. 2, vol. 6, 1896, p. 342; Edwards, Zool. Anz., vol. 19, 1896, p. 108; Edwards, Science, vol. 3, NS, pp. 763-765; Cockerell, Amer. Nat. vol. 30, 1896, p. 226; Herrick, Terry & Herrick, Bull. Sci. Labor. Denison Univ., vol. 11, 1899, pp. 135-136, pl. 19, fig. 16; Bull. Univ. New Mexico, vol. 1, 1899, p. 35; Cope, Rept. U. S. Nat. Mus. for 1898, (1900), p. 432, fig. 77 (*part.*); Gadow, Cambridge Natural History, vol. 8, 1901, pp. 533-534; Stejneger, Proc. U. S. Nat. Mus., vol. 25, 1903, p. 151; Edwards, Science, ser. 2, vol. 27, 1903, p. 826; Stone & Rehn, Proc. Acad. Nat. Sci. Philadelphia, vol. 55, 1903, p. 540; Brown, Proc. Acad. Nat. Sci. Philadelphia, vol. 55, 1903, pp. 552-546; Hurter, Trans. Acad. Sci. St. Louis, vol. 13, 1903, p. 82; Bailey, N. Amer. Fauna, no. 25, 1905, p. 43; Gadow, Proc. Zool. Soc. London, 1905, p. 213; Cragin, Trans. Kansas Acad. Sci., vol. 7, reprint, 1906, p. 114; Ruthven, Bull. Amer. Mus. Nat. Hist., vol. 8, 1907, p. 547, fig. 22; Ditmars, The Reptile Book 1907, p. 153, pl. 46, figs. 9, 13; Strecker, Proc. Biol. Soc. Washington, vol. 21, 1908, pp. 47-52, 72-73, 165-169; Strecker, Baylor Univ. Bull. vol. 12, 1909, pp. 1-9; Hunter & Strecker, Trans. Acad. Sci. St. Louis, vol. 28, 1909, p. 22; Strecker, Baylor Univ. Bull., vol. 13, 1910, p. 7; Gadow, Zool. Jahrb. vol. 29, 1910, p. 706; Ditmars, Reptiles of the World, 1910, p. 151; Stone, Proc. Acad. Nat. Sci. Philadelphia, 1911, p. 229; Lampe, Jahrb. Nassau. Ver. Naturk. vol. 64, 1911, p. 164; Hurter, Trans. Acad. Sci. St. Louis, vol. 20, 1911, pp. 133-135; Bryant, Univ. California Publ. Zool., vol. 9, 1911, p. 5; Ellis & Henderson, Univ. Colorado Studies, vol. 10, 1913, pp. 74-75, pl. 3, fig. 13, Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 3, 1913, p. 392; Winton, Science, NS, vol. 40, 1914, pp. 311, 784; Strecker, Baylor Bull., vol. 28, 1915, p. 23; Winton, Copeia, no. 32, 1916, p. 81-84; Winton, Copeia, no. 39, 1917, pp. 7-8; Weese, Science, NS, vol. 46, 1917, pp. 517-518; Stejneger & Barbour, Check List of the North American Amphibians and Reptiles, 1917, p. 58; Redfield, Copeia, no. 53, 1918, pp. 13-14; Weese, Amer. Nat., vol. 53, 1919; pp. 33-54; Reese, Copeia, no. 103, 1922, pp. 15-16; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, 1922, pp. 409, 420, pl. 35; Strecker, Sci. Soc. San Antonio, Bull. 4, 1922, p. 20; Stejneger & Barbour, Check List

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Phrynosoma harlanii Wiegmann, Herpetologia Mexicana, 1834, p. 54; Duméril & Bibron, Érpetologie Générale, vol. 4, 1837, p. 314; Spring and Lacordaire, Bull. Acad. Roy. Brussels, pt. 2, 1842, p. 192, fig. 2; Duméril and Duméril, Catalogue Methodique de la Collection des Reptiles du Museum d'Histoire Naturelle de Paris, 1851, p. 28.

Phrynosoma orbiculare Holbrook, North American Herpetology, 1 ed. vol. 3, 1838, p. 61, pl. 10 and *idem*, 2 ed. vol. 2, 1842, p. 93, pl. 12.

Phrynosoma (*Tropidogaster*) *cornutum* Fitzinger, Systema Reptilium, 1843, p. 79.

Phrynosoma (*Tropidogaster*) *bufonium* Fitzinger, Systema Reptilium, 1843, p. 79.

Phrynosoma plainceps Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1852, p. 178; Hallowell, *in* Sitgreaves' Expedition down the Zuni and Colorado Rivers, 1853, p. 124, pl. 7; Duméril, Arch. Mus. Hist. Nat. Paris, vol. 8, 1855, p. 552; Aug. Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amerique Centrale, Études sur les Reptiles, livr. 1, 1870, pp. 236-238, pl. 12, figs. 9-9a-f; Bocourt, *idem*, livr. 4, 1874, p. 238; Cope, Bull. U. S. Nat. Mus., no. 1, 1875, p. 49; Yarrow, Report of the Geography and Geology of the Survey West 100th Meridian, under Lt. Wheeler, vol. 5, 1875, p. 579, pl. 24, figs. 1-1b; Coues, *idem*, vol. 5, 1875, p. 593, pl. 24, figs. 1-16; Dugès, La Naturaliza, ser. 2, no. 2, 1896, p. 479.

Phrynosoma cornutum planiceps G. A. Boulenger, Catalogue of the Lizards in the British Museum of Natural History, vol. 2, 1885, p. 246.

Phrynosoma brevicornis E. A. Boulenger, Proc. Zool. Soc. London, 1916, p. 537, pl. 1, fig. 3.

Phrynosoma m'callii Wood, (*nec.* Hallowell), Copeia, no. 1, 1936, pp. 64-70.

Taxonomic history: The species was first named by Harlan (1825) *Agama cornuta.* At least part of the specimens upon which he based his description were in the collection of the Philadelphia Museum of Natural History. Two specimens in particular were mentioned as having been prepared and deposited in the collection. He did not designate a type specimen and gave the distribution as "The Great Plains east of the Rocky Mountains."

When Wiegmann (1828) proposed the generic name *Phrynosoma* he described, along with others, the species *Phrynosoma bufonium* using specimens supposedly from Surinam (Dutch Guiana). Later (1834) he doubted the validity of this locality, especially so after comparing *P. bufonium* with *Agama cornuta* and finding them nearly identical. However, he retained them as separate species, substituting the name *P. harlanii* for *Agama cornuta,* and placing the latter in synonymy. Meanwhile Gray (1831) recognized both *bufonium* and *cornuta,* placing them under *Phrynosoma.*

Duméril and Bibron (1837) recognized that the species *P. bufonium* was identical with *Agama cornuta,* but in their work they followed Wiegmann (1834) and for both species used the name *P. harlanii.* Fitzinger (1843) again recognized two species: *P. cornutum* Gray, under which he placed in synonymy, *Agama cornuta* Harlan and *P. harlanii* Wiegmann; and the second, *P. bufonium* Wiegmann, under which he placed *P. harlanii* of Duméril and Bibron. Fitzinger further grouped the two species into the subgenus *Tropidogaster.* Girard (1852) disregarded Fitzinger's subgeneric division and recognized *P. cornutum* (Harlan) as valid but chose to "lay aside" *P. bufonium* in the absence of authentic locality data. However, he later (1858) placed *P. bufonium* under

P. cornutum, which in turn, he placed in the subgenus *Phrynosoma.* He commented that Fitzinger's *Tropidogaster* had been in use since 1837 for another form and therefore could not be used here. In this same work, Girard placed *P. planiceps* Hallowell under *P. cornutum.* Boulenger (1885) later re-established *planiceps* as a subspecies of *P. cornutum.* Cope (1900) recognized only *P. cornutum.*

Smith and Taylor (1950a) have restricted the type locality of *cornutum* to Fort Riley, Geary Co., Kansas.

Diagnosis: Nostrils within the canthal line; two lateral abdominal scale rows; keeled ventral scales; a single row of enlarged gular scales.

Description: Head as wide as long; snout blunt, forming an acute angle with the frontal area; nostrils large, well within the lines of the canthi, the distance separating them less than diameter of nostril; frontal scales irregular, some pointed and rugose; superciliary ridge terminating posteriorly in a small, erect, often triangular spine; two long occipital spines; a small interoccipital spine; occipital area immediately in front of horns supplied with varying number of small rugose tubercles; temporal areas moderately expanded, projecting posteriorly only as far as, or but slightly farther than, center of occipital area; three temporal spines, middle one usually longest; tympanum not scaled over, although sometimes hidden by fold of skin; three groups of enlarged scales, varying in number, on lateral surface of neck; chinshields eight on each side increasing in size posteriorly and separated from infralabials by one or two small sublabials; a single row of enlarged gular scales on each side; back covered with small imbricate scales, interspersed among varying sizes of enlarged keeled scales; largest scales forming center of dark spots; two rows of slightly enlarged, dark keeled scales paralleling single, medial row of light nonkeeled scales; latter lying exactly above vertebral column; two rows of enlarged pointed scales bordering lateral edge of abdomen; upper row considerably larger than lower; tail edged by single row of peripheral scales equivalent in size to those of abdomen; medium sized, imbricate, keeled scales on anterior and dorsal surfaces of front legs; hind legs bearing dorsally two indistinct rows of enlarged scales with few moderate, imbricate, keeled scales on front of femur; scales of tail much like those of body; ventral scales imbricate, keeled; femoral pores nine to 15 on each side, rows separated mesially by 15 to 20 preanal scales; ground color of head white or light gray, this color replaced on snout by medium brown;

two or three brown to black bands traverse frontal area, the most posterior one connecting superciliary spines; two similar bands on side of head, one extending from eye ventrally, second posterolaterally over temporal area; single pair of large dark brown neck blotches immediately behind head, separated mesially by expanse of light ground-color; three pairs of smaller less definite patches on back, last one being on rump, all more or less outlined by white or gray ground color; dorsal spots each including single large, keeled scale; second but smaller row of spots paralleling first; remainder of back light gray to light tan; tail with single pair of basal spots followed by several dark transverse bands; arms traversed by several dark bands; legs similarly marked; ventral color pinkish gray to white, with numerous dark brown spots over abdomen; tail and limbs uniform light gray.

Variation: The largest specimens are from Texas and Mexico, and are 20 millimeters longer than the largest specimen from Kansas. Specimens from intermediate areas are intermediate in size. Annual length of the feeding period seems to control the size.

The variation in the ground color is considerable, often varying with the substratum upon which the animal lives. The color pattern, however, is more constant, although often varying in distinctness.

Discussion: Of the several forms described that are here regarded as synonyms of this species, there seems to be at least one about which some doubt exists, this being *P. brevicornis* E. G. Boulenger. The description of *brevicornis* was made from a single specimen taken by Prof. J. S. Huxley in Texas and given to Dr. H. G. F. Spurrell for presentation to the Zoological Society of London. It was kept alive in the Societies Gardens where E. G. Boulenger (1916) curator at the Gardens made the description. Burt (1932) placed it in the synonymy of *P. cornutum* upon the evidence received in a letter from Mr. H. W. Parker of the British Museum. Mr. Parker in his letter (quoted by Burt) comments upon a number of abrasions found on the type specimen that were not mentioned by Boulenger. One abrasion he found covered the occipital area and accounted for the short occipital horns that were "worn down or broken off." Accompanying Boulenger's description are three excellent photographs obviously taken of the live animal. On none of these photographs is there any evidence of such an abrasion. Neither do the photographs show clearly the condition of the occipital horns. The photographs would further indicate

Boulenger's interest in the specimen before it died and, if we can believe the photographs, before the abrasions appeared. This is further supported by a note from Mr. Battersby of the British Museum in answer to several of my queries in which he states: "I am afraid I can say nothing definite on the state of the specimen when described by Boulenger. We received it in *July* 1916 [Italics mine] and the paper was received by the Zoological Society for publication on *May* (1916)." The description was in all probability made several weeks prior to its delivery to the "Society," which indicates a period of several months between the time the description was made and the delivery of the specimen to the Museum a period in which the abrasions could have occurred. This does not eliminate the possibility that the horns could have been broken off before the specimen reached the "Gardens." It is not unusual to find specimens in this condition.

Boulenger (*op. cit.*) records the specimen as coming from Texas but mentions no definite locality. Parker (in Burt *op. cit.*) mentions only Texas without further restriction. In reply to my inquiry Prof. Huxley, under date of November 7, 1949, replied as follows:

"I am sorry to say that I have, after nearly 30 years, no recollection of where the specimens you mention were collected. All I can say is that it must have been between Galveston, Austin and San Antonio, as this was the only region of Texas I visited."

Mr. Battersby stated that the locality record (as recorded in the British Museum) was Galveston, Texas.

A comparison of the description and photographs, of *brevicornis* with specimens of *cornutum* from Galveston and surrounding counties show that the two have a majority of their characters in common. The proportions of the head of the two appear to be different although this is not substantiated by actual measurement. The short horns of *brevicornis*, as shown in the photographs, and the failure of Boulenger to mention any abrasions upon the animal, presents a possibility that the specimen might be distinct. However, in view of the conflicting data regarding the type and my failure to locate any specimen that shows exactly the same combination of characters, I am prone to leave it in the synonymy of *cornutum*.

Distribution: The general distribution of this species is from northeastern Kansas and western Missouri, west through most of Kansas, southwest through Oklahoma, Texas, New Mexico to the southeastern part of Arizona, south through the northeastern part

of Sonora into Durango, and east to the Gulf of Mexico. It has been reported from Arkansas and Louisiana. In the latter region, part of the population is known to have been introduced.

Four jaw elements (presumably of this species although positive identification is impossible) are known (Gilmore 1928) from the Conard Fissure, 4 miles west of Willcockson, Newton Co., Arkansas. They are of late Pleistocene Age and are indistinguisable from the corresponding elements of the living animal.

Locality records: Louisiana. *St. Mary Parish:* Morgan City (USNM 25920); South Fork of Red River (Baird & Girard, 1853). *Caddo Parish:* Forbing (introduced) (Strecker & Frierson, 1926); Gayle, 1 mi. S (Frierson, 1927); Shreveport, Wall St. (Frierson, 1927).

Arkansas. *Sebastian Co.:* Fort Smith (Dellinger & Black, 1938).

Kansas. *Allen Co.:* Moran (KU 797-804). *Barber Co.:* Near Dances Cave (KU 19225); Sun City (KU 324-327), 7 mi. S (KU 17913-14). *Bourbon Co.:* (Burt, 1928). *Butler Co.:* Beaumont (KU 334-36). *Chase Co.:* no specific locality (KU 328, 359, 560), (USNM 53208). *Chautauqua Co.:* Cedarvale, 1½ mi. SW (KU 21069). *Clark Co.:* Ashland (AMNH 27238, 36917); Kingsdown, 6 mi. S (KU 22800); Stephenson's Ranch (KU 20229). *Comanche Co.:* Wilmore, 7 mi. NE (KU 20767-68). *Cowley Co.:* Arkansas City (USNM 90694), (KU 12009-018); no specific locality (AMNH 64554); Winfield (USNM 89954-55). *Crawford Co.:* No specific locality (Burt, 1928). *Dickinson Co.:* Carlton (KU 329-333); no specific locality (KU 505). *Elk Co.:* Paw Paw Creek (KU 352); no specific locality (KU 337). *Ellis Co.:* no specific locality (Burt, 1928), (Brennan, 1938). *Ellsworth Co.:* Horsethief Canyon (AMNH 36918). *Geary Co.:* Junction City (USNM 90696), (AMNH 37332); Fort Riley (USNM 6436, 104569-90), (KU 21246). *Greenwood Co.:* Eureka, 8 mi. S (KU 17101); Toronto, 3 mi. SW (KU 16826-29), 8 mi. SW (KU 17422, 16270); no specific locality (KU 356-58). *Harper Co.:* Anthony (KU 348-49); Harper, 5 mi. S (KU 17967-77). *Harvey Co.:* no specific locality (KU 350). *Kingman Co.:* Belmont (Burt, 1935); Zenda, 2 mi. S (KU 19334). *Kiowa Co.:* Rezeau Ranch (KU 21424). *Labette Co.:* Bartlett (KU 322-23); no specific locality (KU 353-54). *Lincoln Co.:* Eylvon Grove, 4 mi. SW (KU 17496); Lincoln (USNM 90695); no specific locality (AMNH 37327), (KU 16912). *Lyon Co.:* no specific locality (Breukelman & Downs, 1936). *McPherson Co.:* Marquette, 5 mi. S (KU 23962); no specific locality (AMNH 37068).

Meade Co.: Meade, 15 mi. SE (AMNH 62837-38); State Line, 1 mi. N (KU 20328); State Park (KU 17633-34). *Mitchell Co.:* Scottsville (AMNH 36916). *Montgomery Co.:* Independence (KU 14650); Wayside (KU 796); no specific locality (KU 339-42). *Morton Co.:* near Elkhart (KU 12023-31); no specific locality (KU 12063-82). *Neosho Co.:* no specific locality (Burt, 1928). *Ness Co.:* no specific locality (Burt, 1928). *Osborne Co.:* no specific locality (Burt, 1928). *Ottawa Co.:* Minneapolis, 3 mi. SW (Burt, 1937); no specific locality (Burt, 1928). *Pawnee Co.:* no specific locality (Burt, 1928). *Phillips Co.:* Glade, 4 mi. S (KU 18601-603). *Pratt Co.:* Cairo (USNM 44687). *Rawlins Co.:* no specific locality (Burt, 1928). *Riley Co.:* no specific locality (AMNH 37325-26). *Russell Co.:* O'Roke (KU 355). *Sedgwick Co.:* Clearwater (USNM 90697). *Seward Co.:* no specific locality (KU 22801). *Smith Co.:* no specific locality (KU 14649). *Sumner Co.:* no specific locality (Burt, 1928); Wellington (KU 323). *Wilson Co.:* Neodesha (AMNH 37331); no specific locality (KU 344-345), (USNM 53409).

OKLAHOMA. *Beckham Co.:* Sayre, 4 mi. S (USNM 92629). *Beaver Co.:* no specific locality (Marr, 1944). *Blaine Co.:* Canton, 5 mi. S (KU 18061-65), 5½ mi. S (KU 18531). *Caddo Co.:* Ft. Cobb (USNM 11831-32). *Carter Co.:* Ardmore (AMNH 7483-87). *Choctaw Co.:* Hugo (KU 16646). *Cimarron Co.:* Boise City (Ortenburger, 1927); Kenton, 3 mi. N (Ortenburger, 1927). *Cleveland Co.:* no specific locality (Ortenburger, 1926). *Comanche Co.:* Wichita Mts. (Ortenburger, 1926). *Cotton Co.:* Junction City 1 mi. SE (Burt, 1935). *Creek Co.:* Drumright (KU 16830-32). *Garfield Co.:* Bison, 1 mi. N (USNM 92623); Enid (USNM 92622). *Hughes Co.:* no specific locality (KU 16646). *Kay Co.:* Ponca City, 1 mi. S (Burt, 1935). *Lincoln Co.:* no specific locality (Ortenburger, 1926). *Logan Co.:* no specific locality (Smith & Acker, 1940). *Major Co.:* Togo, 8 mi. NW (USNM 99452). *Noble Co.:* Sumner, 2 mi. SE (Burt, 1935); near Perry (AMNH 36972-73); Three Sands, 2 mi. S (USNM 99369). *Okfuskee Co.:* Okemah, 3 mi. E (Burt, 1935). *Oklahoma Co.:* Crutcho (Burt, 1935). *Okmulgee Co.:* no specific locality (Ortenburger, 1926). *Pawnee Co.:* Pawnee (AMNH 37329). *Payne Co.:* Stillwater (USNM 53172). *Tulsa Co.:* Tulsa (USNM 89104-08, 125123-24). *Washita Co.:* no specific locality (Ortenburger, 1926). *Woods Co.:* Alva (KU 12056-59).

TEXAS. *Aransas Co.:* St. Josephs Island (USNM 120). *Archer Co.:* Dundee (AMNH 62896-99). *Atascosa Co.:* Benton (KU

12055, 12060-62). *Bastrop Co.:* Bastrop (Cragin, 1884). *Baylor Co.:* Lake Kemp (Strecker & Williams, 1935). *Bee Co.:* Beeville (USNM 44801-02). *Bell Co.:* Temple (Strecker & Williams, 1935); Troy (AMNH 36978). *Bexar Co.:* Near Helotes (KU 11277-78); San Antonio (USNM 10790), (AMNH 20378-81, 44399). *Bowie Co.:* no specific locality (Strecker, 1928 on word of R. C. Cowan). *Brewster Co.:* Alpine (USNM 33007, 33022, 44779-80, 92893); Altuda (USNM 33005); Chisos Mts. (USNM 103631). *Brown Co.:* Brownwood (AMNH 67223-24); Camp Bowie (AMNH 66079-81, 66113-114). *Burnet Co.:* Burnet (KU 267-274). *Castro Co.:* Dimmit (USNM 33012). *Callahan Co.:* Putnam (USNM 71749-50), (KU 12054). *Cameron Co.:* Brownsville (USNM 110, 25403, 52287), (KU 372-73, 11284-87); no specific locality (USNM 17081-82). *Cottle Co.:* Paducah (USNM 92696-703). *Clay Co.:* Henrietta (USNM 33018). *Comal Co.:* no specific locality (Strecker, 1927). *Concho Co.:* Eden, 8 mi. S (Burt & Burt, 1929). *Cooke Co.:* Gainesville (KU 12020-22); no specific locality (USNM 15538-40). *Coryell Co.:* near Cove (Burt & Burt, 1929). *Crosby Co.:* Silver Falls Lake (USNM 92760). *Dawson Co.:* Lamesa, 8 mi. N (KU 12084). *Denton Co.:* Denton (AMNH 36974). *Dimmit Co.:* Carrizo (USNM 33066). *Eastland Co.:* Cisco (KU 484, 394, 395, 398, 12083); no specific locality (Marr, 1944). *Ellis Co.:* Centerpoint (USNM 33013); Redoaks (KU 12085-89); Rockett, 3 mi. S (KU 11393); Waxahachie (USNM 38682). *El Paso Co.:* Ft. Bliss (USNM 4590, 4 spec., 83121-22), (AMNH 38656, 43285-86); El Paso (USNM 33031), (AMNH 15049). *Fisher Co.:* Grady (USNM 29650). *Frio Co.:* near Dilley (KU 11279), 22 mi. W (KU 13190). *Galveston Co.:* Virginia Point (USNM 33028-30); no specific locality (USNM 58562). *Dallas Co.:* Dallas (USNM 17395). *Grimes Co.:* Navasota (USNM 44600). *Hays Co.:* San Marcos (Strecker, 1927). *Hemphill Co.:* Miami, 9 mi. E (KU 16745-48). *Hidalgo Co.:* McAllen (USNM 82296-309), (AMNH 17405-06). *Hill Co.:* Hillsboro, 2 mi. N (AMNH 36977). *Howard Co.:* Big Springs, 9 mi. NW (USNM 92827); Knott, 1 mi. E (USNM 92813). *Houston Co.:* Antioch (USNM 33027). *Hudspeth Co.:* El Paso, 90 mi. below (USNM 143); Ft. Hancock (USNM 20658-61). *Jeff Davis Co.:* Davis Mts. (USNM 33023); Valentine (USNM 33014). *Jim Wells Co.:* Alice (USNM 45042-44). *Johnson Co.:* Grandview 3 mi. S (AMNH 36976). *Kendall Co.:* Waring (USNM 27057); Boerne, 7 mi. W (Strecker, 1926). *King Co.:* Guthrie (USNM 92719-23). *Kinney Co.:* Ft. Clark (USNM 20860-75). *Lipscomb Co.:* Gay-

lord, 5 mi. S (KU 23564-68). *Llano Co.:* Llano (USNM 33011). *McLennan Co.:* Waco (KU 11280-83, 12008); no specific locality (USNM 59029). *Martin Co.:* Stanton (USNM 92323-29). *Medina Co.:* Castorville (Strecker & Williams, 1935). *Menard Co.:* London, 4 mi. NE (USNM 83683). *Mitchell Co.:* Colorado (AMNH 6834-45). *Nueces Co.:* Corpus Christi (USNM 33019, 45304-56, 47702). *Oldham Co.:* Tascosa (USNM 33016). *Randall Co.:* near Umberger (KU 6542). *Reeves Co.:* Toyahvale (USNM 33004). *Refugio Co.:* no specific locality (Strecker, 1908). *Pecos Co.:* Ft. Stockton (USNM 5181, 33024, 92873). *Presidio Co.:* Marfa (USNM 47700). *Shackelford Co.:* no specific locality (USNM 12616). *Starr Co.:* Rio Grande City (USNM 33003), (KU 11276); Roma (USNM 33020). *Taylor Co.:* Abilene (AMNH 64786, 65470); Camp Barkley (BYU 6054-57). *Terrell Co.:* no specific locality (KU 13191). *Tom Green Co.:* San Angelo (AMNH 65305). *Travis Co.:* Austin (USNM 13465-69). *Val Verde Co.:* Comstock, 12 mi. E (AMNH 66056). *Victoria Co.:* Victoria (USNM 78549). *Webb Co.:* Laredo (KU 11273-75), (USNM 7123, 86901). *Wichita Co.:* Wichita Falls (USNM 45041), (AMNH 7498-7524); no specific locality (USNM 42303). *Williamson Co.:* no specific locality (Milne, 1938).

NEW MEXICO. *Chaves Co.:* Roswell (USNM 33009, 93006-07). *Dona Ana Co.:* Jornada Exp. Range (USNM 100885-86, 102234); La Cruces, 25 mi. N (KU 21410); Las Cruces (KU 17659); Organ Pass, E side (USNM 25430). *Eddy Co.:* Carlsbad (USNM 33008), (KU 12032-39). *Grant Co.:* Dog Springs (USNM 21011-13, 31015-17); Hachita (USNM 45099); Hurley (AMNH 28362). *Guadalupe Co.:* Santa Rosa (USNM 33010), (AMNH 44952). *Hidalgo Co.:* Animas Valley (USNM 45068, 45078); Lordsburg (USNM 92998-99). *Lea Co.:* Lovington (USNM 94357). *Luna Co.:* Deming (USNM 80073), (AMNH 66055), (KU 375); Silver City, 29 mi. SE (KU 6543). *Otero Co.:* Alamagordo (AMNH 539-46). *Quay Co.:* Tucumcari (KU 20530). *Rio Arriba Co.:* Abiquiu (Van Denburgh, 1924). *Socorro Co.:* Magdalina (KU 377); San Marcial (USNM 45070). *Union Co.:* Rabbit Ear Mts. (AMNH 62862); no specific locality (KU 12019). *Taos Co.:* Taos (Van Denburgh, 1924). *Mora Co.:* Ft. Union (Van Denburgh, 1924). *Santa Fe Co.:* Ildefonso (Van Denburgh, 1924); Santa Fe (Van Denburgh, 1924). *Sierra Co.:* Lake Valley (Van Denburgh, 1924).

ARIZONA. *Cochise Co.:* Benson, 9 mi. W (Klauber, 1939); 18 mi. NE (AMNH 68457-58); Bisbee (AMNH 1281); Bowie (USNM 8438); Douglas (KU 6963, 376), 22 mi. S (AMNH 63494), 27 mi. N (AMNH 66053-56); Ft. Huachuca (USNM 21001); San Pedro River (USNM 20564, 21019-20); Wilcox (USNM 22235), 12 mi.

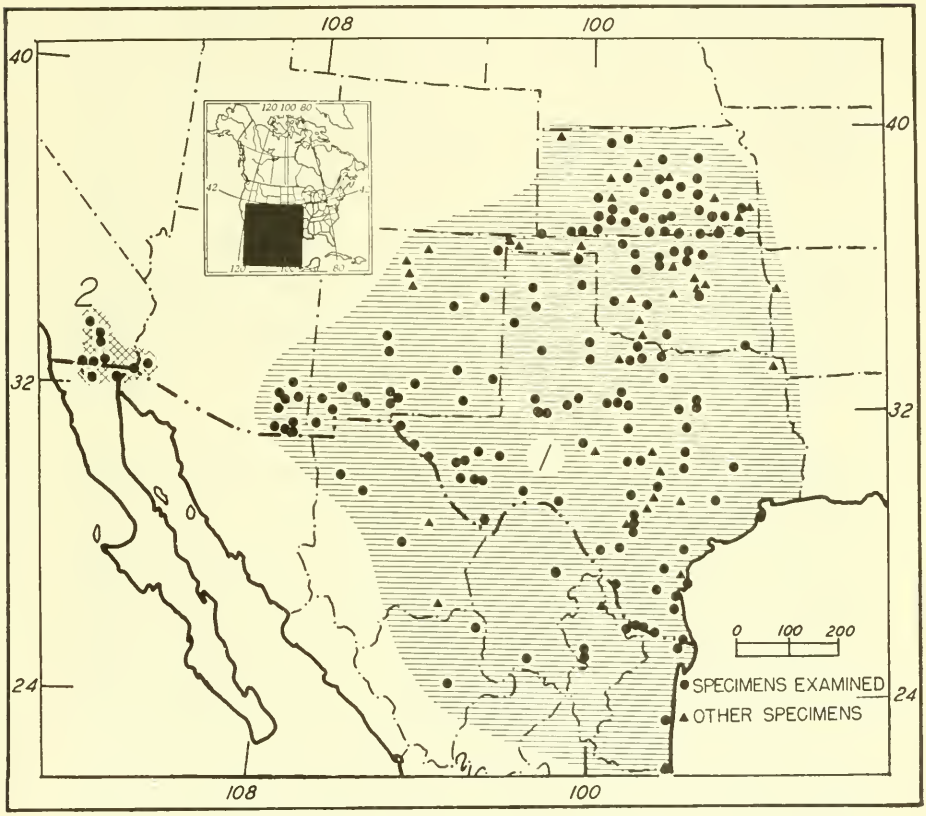

FIG. 7. Map showing the geographic distribution of the species: 1. *Phrynosoma cornutum*, and 2. *Phrynosoma m'callii.*

NW (USNM 44565). *Graham Co.:* SE Ariz. (USNM 8576); no specific locality (KU 21935).

MEXICO. *Chihuahua:* Allende (Schmidt & Owen, 1944); Ascensión, 27 mi. N (USNM 104692); Casas Grandes, (USNM 47475-77), 10 mi. EE. (USNM 104693-704), 14 mi. E. (USNM 104705); Chihuahua (city?) (USNM 14290, 14300, 64433-4); Hacienda La Babia (Sierra del Carmen), (Schmidt & Owen, 1944); Hacienda La Mariposa (Schmidt & Owen, 1944); Hacienda El Zacate

(Schmidt & Owen, 1944); Moctezuma (USNM 65831); 30 mi. N (KU 20528); Muzquiz (Schmidt & Owen, 1944); Rio Santa María near Progreso (USNM 104706-712); San Buenaventura, 12 mi. E (USNM 105310-11); San Juan (Schmidt & Owen, 1944); Santa Marcia (USNM 47173-79); Santa Rosa (USNM 47356-59); Villa Acuña (Schmidt & Owen, 1944); White Water Monument (USNM 21007-10). *Durango:* Bermejillo, 25 mi. N (KU 19255); San Juan del Río (AMNH 68341); La Loma, 7 mi. S (Smith, 1934); Lerdo, 15 mi. SW (AMNH 67450); Between Torreon & Bermejillo (KU 20529, 19254). *Sonora:* Sonora Mex. (USNM 92579). *Coahuila:* Álamos de Parras (USNM 114); Castañuelas (USNM 113); Las Delicias, 10 mi. E (AMNH 67382), 17 mi. S (AMNH 67381); Patos (USNM 112); Sabinas (USNM 47836). *Nuevo León:* Monterey (USNM 117), 20 km. N (USNM 111364); Nuevo Laredo, 25 mi. S (Smith, 1934); Santa Catarina (USNM 47835). *Tamaulipas:* Marmolejo (Gaige, 1932); Matamoros (USNM 107); Mier (USNM 47165-67); Soto la Marina (USNM 47834); Tampico (Günther, 1885).

Phrynosoma solare Gray

Phrynosoma solaris Gray, Catalogue of the Specimens of Lizards in the Collection of the British Museum of Natural History, 1845, p. 229; Van Denburgh, Proc. California Acad. Sci., ser. 2, vol. 4, 1894, p. 456.

Phrynosoma regale Girard, Report of the United States Exploring Expeditions during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes USN, vol. 20, 1858, Herpetology, p. 406; Baird, United States Mexican Boundary Survey under the order of Lieut. Col. W. H. Emory, Reptiles of the Boundary, vol. 2, 1859, p. 9, pl. 28, figs. 1-3; Cope, Proc. Acad. Nat. Sci. Philadelphia, 1866, pp. 202-203; Aug. Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 1, 1870, pl. 12, figs. 12a-f, and Bocourt *idem*, livr. 4, 1874, pp. 235-236, pl. 12, figs. 12a-b; Cooper, Proc. California Acad. Sci., vol. 4, 1870, p. 67; Cope, Bull. U. S. Nat. Mus., no. 1, 1875 p. 49; Yarrow, Report of the Geography and Geology of the Surveys West of the 100th Meridian, under Lt. Wheeler, vol. 5, 1875, Zoology, p. 578; Coues, *idem*, 1875, p. 593; Müller, Verh. Naturf. Gesell. Basel, 1878, p. 634; Lockington, Amer. Nat. vol. 14, 1880, p. 295; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, pp. 11, 66; Boulenger, Catalogue of the Lizards in the British Museum of Natural History, vol. 3, 1885, p. 245; Gentry, Proc. Acad. Nat. Sci., Philadelphia, 1885, p. 146; Ditmars, The Reptile Book, 1907, p. 150, pls. 46, figs. 11, 15, and 49, fig. 1; Ditmars, Reptiles of the World, 1910, pp. 151-152; Stone, Proc. Acad. Nat. Sci. Philadelphia, 1911, p. 229.

Phrynosoma solare Van Denburgh, Proc. California, Acad. Sci., ser. 2, vol. 5, 1895, p. 115; Van Denburgh, *idem*, vol. 6, 1896, p. 342; Cope, Report U. S. Nat. Mus. for 1898 (1900), p. 420, fig. 73; Ruthven, Bull. Amer. Mus. Nat. Hist., vol. 23, 1907, pp. 544-546, fig. 21; Bryant, Univ. California Publ. Zool., vol. 9, 1911, p. 5; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 3, 1913, pp. 392, 406; Stejneger and Barbour, Check List of North American Amphibians and Reptiles, 1917, p. 60; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 11, 1921, p. 51; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, vol. 1, 1922, pp. 406-409; pl. 34, figs. 1-2; Nelson, Mem. Nat. Acad. Sci., vol. 16, 1922, p. 114;

Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 2 ed., 1923, p. 63; Ortenburger, Proc. Oklahoma Acad. Sci., vol. 6, 1926, p. 108; Burt & Burt, Journ. Washington Acad. Sci., vol. 19, no. 20, 1929, pp. 454-455; King, Copeia, no. 4, 1932, p. 177; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 69; Allen, Occas, Papers Mus. Zool. Univ. Michigan, no. 259, 1933, p. 10; Burt, Amer. Midl. Nat., vol. 14, 1933, p. 245; Taylor, Univ. Kansas Sci. Bull., vol. 24, 1936, p. 484; Gloyd, Bull. Chicago Acad. Sci., vol. 5, 1937, p. 113; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed., 1939, p. 75; Little, Copeia, no. 4, 1940, p. 263; Driver, Name That Animal, 1942, p. 348; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 95; Kauffeld, Amer. Midl. Nat., vol. 29, 1943, p. 345; Schonberger, Copeia, no. 1, 1945, pp. 53-54; Bogert & Oliver, Bull. Amer. Mus. Nat. Hist., vol. 83, 1945, pp. 303-420; Smith & Laufe, Trans. Kansas Acad. Sci., vol. 48, 1945, p. 337; Vorhies, Copeia, no. 4, 1948, p. 303; Edgren, Copeia, no. 2, 1948, p. 129; Smith and Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, p. 355; Bull. U. S. Nat. Mus., no. 199, 1950, p. 104.

Taxonomic history: Gray (1845) in his Catalogue of Lizards of the British Museum named *Phrynosoma solaris* from a specimen in the British Museum of Natural History from "California." His description, a single line, appearing under his discussion of *P. coronatum*, was sufficient to characterize the species. Girard (1852) does not mention this species or Gray's work. Later (1858) however, he placed *P. solaris* Gray in the synonymy of his *Batrachosoma coronatum* and described as new a species *P. regale.* Bocourt (1874) does not mention *P. solaris Gray,* but does list *P. regale* Girard as valid. Van Denburgh (1894) was the first to point out the validity of Gray's description and thus placed *P. regale* in synonymy. Cope (1900) after examining the type specimen reluctantly accepted Gray's one-sentence description and synonymized *P. regale.*

Diagnosis: One of the largest species in the genus, *P. solare* can be identified by the following characteristics: two pairs of occipital spines, which with the large temporal spines form a continuous series on posterior limits of head; nostrils within canthal line; two scale rows in lateral abdominal fringe; ventral scales keeled.

Description: Head slightly longer than wide, bearing posteriorly two pairs of occipital and four pairs of temporal spines, arranged in a continuous series; nostrils within the canthal lines; rostrum blunt; rostrofrontal angle abrupt; superciliary ridges prominent, ending posteriorly in a broad, pyramidlike scale; chinshields approximately eight on each side, increasing in size posteriorly; one incomplete row of sublabials between infralabials and chinshields; gular scales small; one row of enlarged scales extending from level

of fourth chinshield to gular fold; two distinct groups of enlarged scales on side of neck; tympanum exposed; dorsal scales generally small; eight dorsal longitudinal rows of enlarged scales on back, four extending onto the tail; one scale row in abdominal fringe; abdominal scales proportionately small and keeled; femoral pores 17 to 19 on each side.

Dorsal ground color grayish tan to reddish; neck blotches dark brown to black, often extending posteriorly along lateral portion of back; paravertebral spots irregular, often appearing as undulating broken bands, usual light borders often missing; tail traversed by narrow dark bands; head yellowish tan with points of larger scales often dark; ventral area with scattered dark spots.

Variation: The large head spines vary in length and in the angle at which they diverge from each other; however, two occipitals and four temporals are always present on each side. The fourth temporal may be reduced in size and appear as an enlarged scale at the base of the third. The keeling may be distinct upon all the ventral scales or it may be absent on all but a few scales in the area between the front legs. Size and age seem to have no effect upon the presence or absence of the keeling. The femoral pores vary from 15 to 23 on each side and from one to six preanal scales separate the femoral pore-rows mesially.

The ground color varies with the substratum but the dorsal pattern is usually clearly discernible. It is faint in some specimens.

Remarks: This species is one of the largest found in the genus. Three specimens (KU ♀ 22798, ♀ 22787, ♀ 396) have snout-vent measurements of 117, 115, and 114 mm. respectively; the total length of the largest (KU 22798) being 163 mm. (approx. 6½ inches). Ortenburger (1926) and Smith (1946) have suggested that the species might be divisible into several subspecies. Analysis of the material available for this study fails to give basis for such a division.

Distribution: The general distribution of this species is through the central part of Arizona, southwestward to the Colorado River, south into Sonora, following the Gulf of Mexico into Northern Sinaloa and north to the southeast corner of Arizona. Smith and Taylor (1950a) have restricted the type locality to Yuma, Yuma Co., Arizona.

Locality records: ARIZONA. *Cochise Co.:* Huachuca Mts., Romero Canyon (KU 6968). *Graham Co.:* Whitlock Mts. near Natural Gate (MVZ 23989). *Gila Co.:* Globe (MVZ 6308); Payson,

20 mi. S (MVZ 2243); no specific locality (MVZ 21932). *Maricopa Co.:* Higley (USNM 63047); Phoenix (KU 11319-21, 22786-87), (USNM 37962, 46223, 71523); Wickenburg (USNM 89954); no specific locality (KU 21933). *Pima Co.:* Benson, 12 mi. W (MVZ 8185); Nogales, 30 mi. N (MVZ 10169); Santa Catalina Mts., Sabino Canyon (KU 11317-18); Tucson (USNM 17170, 118588-89, 84257, 85966), (BYU 8047), 30 mi. S (EHT-HMS 10436); no specific

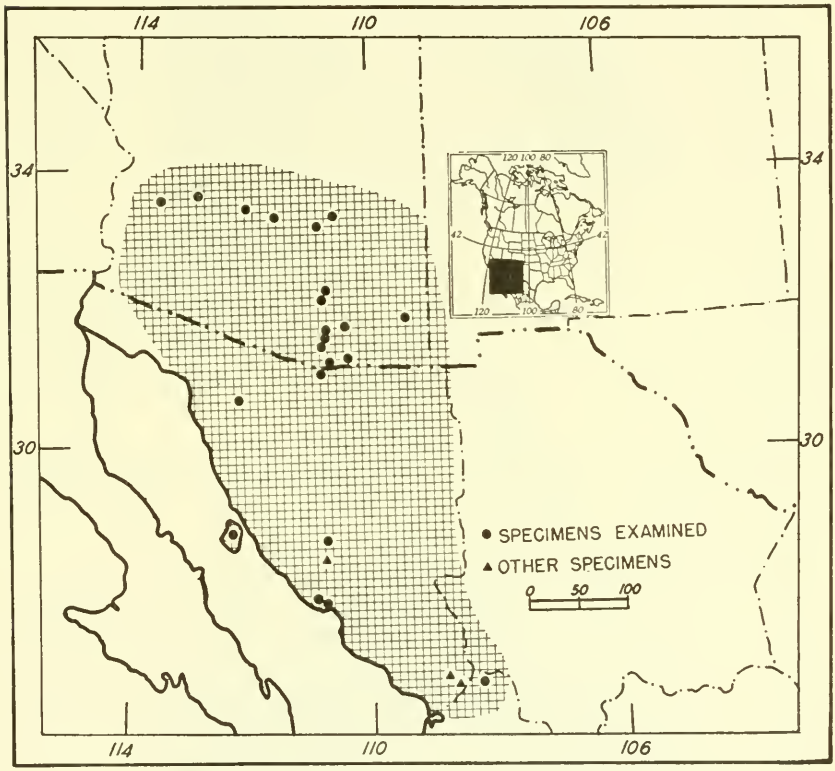

Fig. 8. Map showing the geographic distribution of the species *Phrynosoma solare.*

locality (USNM 61380, 2 spec.). *Pinal Co.:* Superior (EHT-HMS 10435). *Santa Cruz Co.:* Nogales (MVZ 62059); Tubac (MVZ 20541). *Yuma Co.:* Harquahala Mts. (USNM 60175-76).

Mexico. *Sonora:* Álamo Muerto, 30 mi. NW Cabonea (MVZ 10167-68); Álamos (Bogert and Oliver, 1945); Empalme (EHT-HMS 10439); Guaymas (EHT-HMS 10440); Guirocoba (Bogert and Oliver, 1945); Hermosillo, 8 mi. S (EHT-HMS 10437), 15-20 mi. S (Allen, 1933); La Posa, 1 mi. W (EHT-HMS 10438); Nogales

(USNM 62075, 62256); Sierra de la Nariz, near Zuñi (USNM 161); Santa Ana (EHT-HMS 10441); Tiburón Islands, no specific locality (USNM 48148). *Sinaloa:* Sierra de Choix (USNM 47541). *Baja California:* Las Ánimas Bay (Lockington, 1880*).

Phrynosoma taurus Dugès

Phrynosoma taurus, Dugès, Desc. Manuscript (*fide* Duméril and Bocourt *loc. cit.*, p. 234), 1869; and La Naturaleza, 1869, p. 143 (*nomen nudum*); Aug. Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles livr. 1, 1870, pl. 12, figs. 8, 8a-g; Bocourt, *idem,* livr. 4, 1874, pp. 234-235, pls. 1, 2, figs. 8a-g; Dugès, La Naturaleza, 1873, pp. 302-305, figs. 1-4; Boulenger, Catalogue of Lizards in the British Museum of Natural History, vol. 2, 1885, p. 249; Ditmars, Reptiles of the World, 1910, p. 151; Ruthling, Copeia, no. 72, 1919, pp. 67-68; Smith & Necker, Anales de la Escuela Nacional de Ciéncias Biologica, vol. 3, nos. 1-2, 1943, pp. 208- 210, figs. 1-2; Smith & Laufe, Trans. Kansas Acad. Sci., vol. 48, 1945, p. 337; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, p. 341; Bull. U. S. Nat. Mus., no. 199, 1950, p. 104.

Taxonomic history: Dugès (1869) described this species from specimens in Mexico, and sent the manuscript to Aug. Duméril in Paris. In Paris a figure was made from one of nine specimens housed there and the figures were published under the name *Phrynosoma taurus* Dugès. The species has never been placed in any other genus.

Diagnosis: Nostrils within the canthal lines; one row of lateral abdominal spines; ventral scales keeled throughout; temporal shelf greatly extended posterolaterally terminating in a heavy, moderately long temporal spines.

Description: Head slightly broader than long; frontal areas inclined sharply forward and bordered by prominent superciliary ridges terminating posteriorly in an enlarged superciliary spine; nostrils located within canthal lines, of moderate size, separated from each other by a distance equal to one or one and one-half times diameter of nasal openings; occipital spines small; temporal area much enlarged posterolaterally, terminating in two, moderately long spines; outer larger and longer than inner; temporal spine far exceeding occipital in backward projection; scales of temporal area increase in size toward temporal spines; tympanum exposed; supralabials and infralabials small, latter separated from chinshields by one or two small sublabials; chinshields keeled, moderately pointed, increasing in size posteriorly; one slightly en-

* There have been no additional specimens taken in Baja California, the nearest being those collected in Yuma Co., Arizona, and Sonora, Mexico. The occurrence of this species in Baja California is gravely doubted.

larged row of scales on either side of gular area; gular fold covered posteriorly by minute scales; neck fold expanded and bearing series of enlarged scales; second smaller fold joining first posteriorly; numerous enlarged, keeled scales scattered over back; single lateral abdominal row borne anteriorly on fold of skin originating

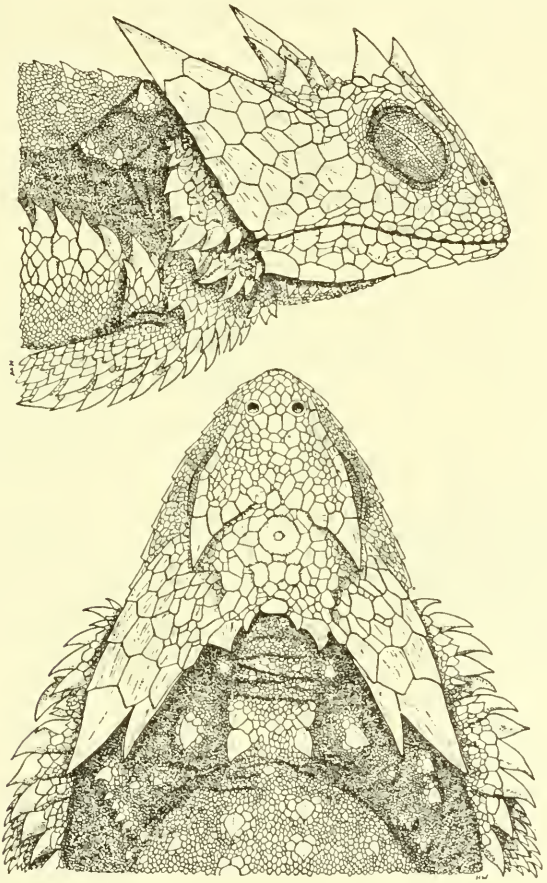

Plate XC. *Phrynosoma taurus* Dugès. EHT-HMS No. 23987, 5 mi. N Chilpancingo, Guerrero, Mexico.

on shoulder above arm; fold diminishing posteriorly and disappearing at about one half to two thirds body length; tail short, approximately equal to, or less than, length of head; ventral scales keeled throughout; femoral pores numbering from ten to twelve on each side; rows separated mesially by approximately 20-23 preanal scales. Head olive, body slightly darker gray; neck

blotches dark gray with three pairs of faint blotches on body posterior to them; single faint band traversing tail; faint dark spots scattered over ventral area.

Discussion: This species is one of the most distinctive of the genus. The prolongation of the supratemporal areas is distinctly

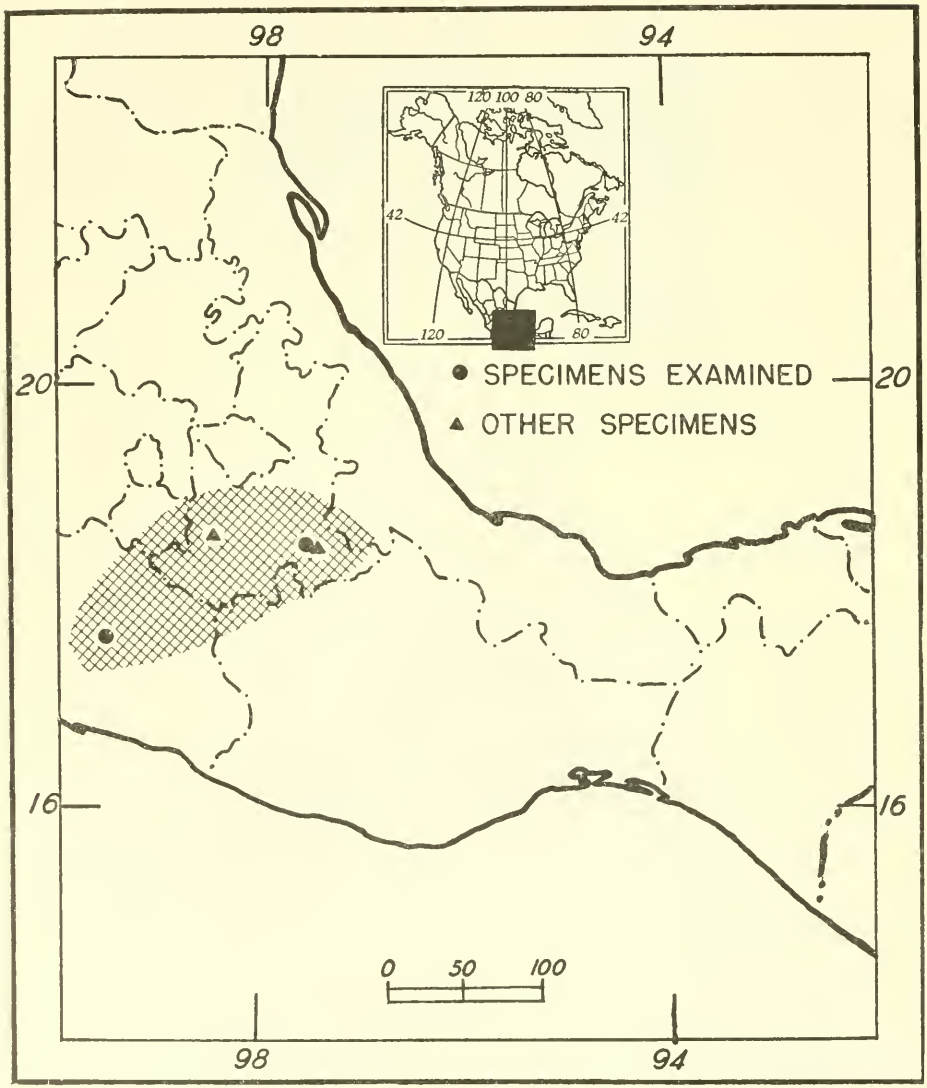

FIG. 9. Map showing the geographic distribution of the species *Phrynosoma taurus*.

greater than in any other form. Its affinities seem to be remotely with *douglassii.*

Locality records: Mexico. *Puebla:* Cacoloápam (EHT-HMS 22246); Cozcatlan, near Tehuacán (Anales de la Escuela Nacional de Ciéncias Biologia); Izúcar de Matamoros (9 spec. Mus. d'Hist. Nat. Paris); San Diego (USNM 11368). *Guerrero:* Chilpancingo, 5 mi. N (EHT-HMS 23987).

Phrynosoma douglassii brevirostre Girard

Tapaya° *brevirostris* Girard, *in* Report of the Exploring Expeditions during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, USN, vol. 20, Herpetology, 1858, p. 397; Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 4, 1874, pp. 285-289.

Phrynosoma brevirostre Cope, Proc. Acad. Nat. Sci. Philadelphia, 1866, p. 302; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 1917, p. 58; Stejneger & Barbour, *idem,* 2 ed., 1923, p. 60; Burt, Copeia, 1927, pp. 53-54; Burt, Trans. Acad. Sci. St. Louis, vol. 27, 1928, p. 32; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 66; Stejneger & Barbour, *idem,* 4 ed., 1939, p. 72; Hudson, Nebraska Conservation Bull. no. 24, 1942, pp. 36-38; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, pp. 91-92; Wheeler, Amer. Midl. Nat., vol. 38, 1947, p. 181.

Phrynosoma douglassii douglassii Cones & Yarrow, Bull. U. S. Geology and Geography Surveys west of the 100th Meridian under Lieut. Wheeler, vol. 5, Zoology, 1878, pp. 285-287.

Phrynosoma hernandesi Stone, Proc. Acad. Nat. Sci. Philadelphia, 1911, p. 229.

Phrynosoma douglassii hernandesi Cope, Rept. U. S. Nat. Mus. for 1898 (1900), pp. 413-415 (*part.*); Over, South Dakota Geol. and Nat. Hist. Surv. Bull., vol. 12, 1923, p. 19; Brennan, Trans. Kansas Acad. Sci., vol. 37, 1934, p. 190; Burt & Hoyle, Trans. Kansas Acad. Sci., vol. 37, 1934, p. 201.

Phrynosoma douglassii ornatissimum Burt, Trans. Acad. Sci. St. Louis, vol. 26, 1928, pp. 32-36, fig. 6.

Phrynosoma orbiculare brevirostre Klauber, Bull. Zool. Soc. San Diego, no. 14, 1939, p. 93.

Phrynosoma douglassii brevirostre Smith, Handbook of Lizards, 1946, pp. 302-304, pl. 79; Maslin, Univ. Colorado Mus. Leaflet, no. 3, 1947, pp. 5, 11.

Taxonomic history: This subspecies was first named by Girard (1858) from specimens in the United States National Museum. He placed it in the subgenus *Tapaya.* The distributional data accompanying the description was merely the "plains of Kansas and Nebraska." To my knowledge a type specimen has never been designated, although number 208 of the United States National Museum collected by S. W. Wood at Pole Creek, Nebraska, is recorded as the type in the cards at that Museum. In view of the above, I here designate USNM 208 as the type of *Tapaya brevirostris* Girard, and restrict the type locality to Pole Creek (now Lodge Pole Creek) near Dix, Kimball Co., Nebraska. Smith (1946) made *brevirostre* a subspecies of *douglassii.*

° Actually considered as a subgenus, hence Girard has no parentheses.

Diagnosis: Temporal spines shorter than their basal diameter; head width at angle of jaw exceeding that of temporal area; dorsal spots indistinctly bordered or bordered only on posterior edges by lighter color.

Description: Size small; head wider than long, frontal area slightly convex, covered with small, irregular, rugose scales; superciliary ridges prominent, terminating in short, blunt, triangular spines; nostrils on canthal line, of medium size, separated by a distance equal to four or four and one-half times diameter of one nostril; temporal shelf expanded, convex; temporal spines small, shorter than their basal diameters, projecting vertically; interoccipital spine absent; occipital shelf bearing several small tubercles; supralabials small, inconspicuous; three posterior infralabials slightly enlarged, continuous with the three enlarged postlabials; chinshields small, separated from infralabials by two small sublabials; gular scales small, equal; two lateral neck patches of enlarged soft spines, lower patch smaller; tympanum exposed dorsal scales minute, smooth, imbricate; six to eight indistinct longitudinal rows of enlarged keeled scales; one row of slightly enlarged, soft scales forming lateral abdominal fringe; two rows of enlarged scales on tail; ventral scales of medium size, imbricate, smooth; femoral pores 15-15, rows separated mesially by five preanal scales.

Dorsal ground color gray to dark gray; nuchal blotches indistinct; dorsal dark spots fading into ground color, bordered by a lighter color only on posterior side; several pairs of indistinct dark spots on tail, these becoming transverse bars toward tip; head brownish gray with a few black flecks on frontal area; ventral scales cream, sparsely flecked with black.

Variation: The variation in this form is exceedingly great. Individuals can be found well within the geographic range of this subspecies, which resemble those of any one of the other subspecies of *douglassii*. A majority of the specimens, however, agree generally with specimens from the type locality. The rostrum varies from the typical blunt condition with the nostrils directed somewhat forward to a more pointed rostrum with lateral nostrils. The occipital spines vary in size and the direction in which they project from the skull. The dark dorsal spots may be edged with light scales posteriorly or they may be entirely absent. In the part of the range meeting that of *ornatissimum*, a few of the spots will have light mesial borders.

Discussion: This subspecies is most closely related to *P. d. ornatissimum* as is shown best in the characteristics of the occipital and temporal regions of the head. The temporal spines are short and usually project upward. Their lateral profile closely resembles that of *ornatissimum,* as does the thick expanded appearance of the lateral temporal area. The occipital spines are equivalent to those of *ornatissimum* in size, shape, the angle at which they are attached to the skull, and the interoccipital distance between them. The differences in the two lies in the smaller size of *brevirostre,* the reduction of the white borders of the dorsal spots and the general "faded" condition of the dorsal pattern as a whole.

Locality records: Colorado. *Boulder Co.:* Boulder (USNM 34569-70). *Denver Co.:* Denver (USNM 30915-20, 29601). *El Paso Co.:* Colorado Springs (USNM 8444, 5 spec., 9263, 8514); *La Plata Co.:* no specific locality (USNM 35469). *Moffet Co.:* Lay (USNM 40141); Snake River (USNM 40144). *Weld Co.:* no specific locality (KU 23571-72); Greeley (USNM 37035); Avalo (USNM 40139). *Morgan Co.:* no specific locality (KU 370-371).

Kansas. *Edwards Co.:* no specific locality (Burt, 1928). *Ellis Co.:* Fort Hays (Brennan, 1934). *Geary Co.:* Ft. Riley (USNM 4612). *Logan Co.:* no specific locality (KU 366), (AMNH 36911). *Rooks Co.:* no specific locality (Burt, 1928). *Smith Co.:* no specific locality (KU 506).

Montana. *Chouteau Co.:* Fort Benton (USNM 9414). *Gallatin Co.:* Gallatin Station (USNM 17415); Logan (USNM 32652), no specific locality (USNM 14641). *Garfield Co.:* Cohagen, 25 mi. SW (USNM 44931). *Golden Valley Co.:* Painted Robe (USNM 45299). *Hill Co.:* Milk River at Lat. 49° (USNM 1148). *Prairie Co.:* Terry 25 mi. N (USNM 44931). *Richmond Co.:* Mouth of Yellowstone River (USNM 9198). *Rosebud Co.:* Rosebud Creek (USNM 45300-301). *Yellowstone Co.:* Billings (USNM 44705, 44929-30), East Pryor Creek (USNM 28443-45), Fort Custer (USNM 14523).

Nebraska. *Box Butte Co.:* Hemingford (NSM R151-157, R358-359, 983, 1081), 5 mi. N (NSM R311-312); no specific locality (KU 21451-52). *Cherry Co.:* Valentine, 3 mi. SE (Burt & Hoyle, 1934).* *Cheyenne Co.:* Sidney (USNM 10786). *Dawes Co.:* Crawford (NSM 1190-92); Dunlap, 14 mi. W (AMNH 60054-58); Wayside

* Hudson, 1942, p. 37 corrects this record, stating that the specimen actually came from Sioux County.

(KU 23082). *Kimball Co.:* Dix (NSM R354-357); Pole Creek (= Lodge Pole Creek) (USNM 208). *Scottsbluff Co.:* Gering (AMNH 64738-40). *Sheridan Co.:* Hay Springs (AMNH 58966, 60296), 12 mi. SW (NSM 429). *Sioux Co.:* Agate (NSM R168-170, R310); Andrews (NSM R143-147); Henry, 18 mi. N (NSM R220); Niobrara River (AMNH 64714, 64751-57), 9 mi. N (AMNH 64750); Orella (NSM 1189).

SOUTH DAKOTA. *Fall River Co.:* Ardmore (USNM 63047). *Harding Co.:* Crow Buttes (Over, 1923). *Shannon Co.:* Wounded Knee Creek (Over, 1923). *Washington Co.:* Wounded Knee Creek (Over, 1923).

NORTH DAKOTA. *Billings Co.:* Peaceful Valley Ranch (Wheeler, 1947); near Medora (Wheeler, 1947); Mikkelson (Wheeler, 1947). *Golden Valley Co.:* Beach (Wheeler, 1947). *McKenzie Co.:* "40 miles N of Sentinel Butte" (Wheeler, 1947).

WYOMING. *Big Horn Co.:* Burlington (USNM 48181-82). *Carbon Co.:* Fort Steele (USNM 48154); Saratoga (USNM 48110-11); 12 mi. N (AMNH 58842). *Fremont Co.:* Washakie (USNM 44788-92). *Goshen Co.:* Fort Laramie (USNM 4604, 2 spec.). *Park Co.:* Cody (USNM 48178-80). *Platte Co.:* Cassa (USNM 40190). *Natrona Co.:* Powderville (USNM 54591-93). *Sheridan Co.:* Sheridan (USNM 47704). *Hot Springs Co.:* Owl Creek Mountains (USNM 48122-23). *Sweetwater Co.:* Bitter Creek, 18 mi. S (KU 23091), 24 mi. S (AMNH 46994); Black Rock Butte (USNM 49666); Green River (Stone, 1911). *Uinta Co.:* Bridger Pass (USNM 9313, 9308, 16018); Evanston, 14 mi. N (USNM 48686); Fort Bridger (USNM 47703, 5455, 44913); 8½ mi. W (KU 23594); Weston, 23 mi. SW (KU 23680-81). *Washakie Co.:* Ten Sleep, 20 mi. W (USNM 48183-84, 48124).

Phrynosoma douglassii brachycercum Smith

Phrynosoma douglassii brachycercum Smith, Proc. U. S. Nat. Mus., vol. 92, 1942, pp. 362-363; Smith, Trans. Kansas Acad. Sci., vol. 48, 1945, p. 338; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, pp. 330, 375; Bull. U. S. Nat. Mus., no. 199, p. 100.

Taxonomic history: Smith (1942:362) named this form from specimens in the United States National Museum, taken in Durango, Mexico by Dr. Edward Palmer.

Smith's diagnosis and description are repeated here:

Diagnosis: "Similar to *Phrynosoma douglassii*, but with a tail shorter than head is wide or in adults, very slightly longer; gular scales in straight rows slightly diverging posteriorly, the scales small

and tubercular (strongly convex), not flat; chest scales keeled; horns of head very short, postorbitals, temporals, and occipitals subequal in size.

"Description of holotype.—Head a broad, short, conventionalized heart-shape in profile; in lateral profile, postorbital spine highest, supraocular and internasal areas forming an obtuse angle with each other (not a curve); width of head (26.2 mm.) at widest point in temporal region much greater than length of head from snout to occiput (15.6 mm.) or to posterior tip of temporal spine (21 mm., in a projected straight line); supraocular [frontal] region flat, with no enlarged scales; posterior border of supraocular [frontal] region strongly indented medially, marked by a series of enlarged, slightly protuberant scales; each series begins at postorbital [superciliary] spine and extends anteriomedially, but fails to reach its mate by 1 scale; postorbital [superciliary], occipital, and temporal spines subequal in size; 5 scales between occipital spines; 2 small, flat spines, separated from each other by a scale, preceding occiput; 3 subequal temporal spines, the posterior slightly separate from others, the series continuing anteriorly as a row of enlarged scales, disappearing below about the middle of the eye.

"Three posterior infralabials [postlabials] considerably enlarged, keeled scales [chinshields] in contact with a few infralabials anteriorly but separated throughout the remainder of its length by one to three rows of small scales; gulars in very definite, straight rows slightly diverging posteriorly; these scales not flat, but small and convex (tubercular); in extreme posteriolateral portion of throat the scales are strongly protuberant and conical, and have no free lateral edges.

"An irregular series of preauricular spines; tympanum exposed; a large skin fold anterior to lateral nuchal pocket, and a small one posteriorly, the former surmounted by two series of spines, the latter by one or two spines; a small, vertical series of spines in front of the above arm insertion.

"All dorsals keeled, imbricate (except enlarged spines), not granular; among these are scattered, enlarged keeled spines of varying size, diminishing laterally; a single row of lateral spines (fringe); in the posterior part of the fringe the spines are separated from each other, while anteriorly they are in contact; spines on tail few, small; tail very broad at base, but remainder very slender, not tapering into base; eight longitudinal series of spines at base of tail.

"Scales on chest rather distinctly keeled; remainder of ventral

scales smooth; femoral pores 16-18; 14-16 lamellae under fourth toe. Total length 80 mm.; tail 24 mm.

"Head slightly reddish; body dirty straw yellow, with transverse, medium, dusky (gray) crossbands; limbs feebly barred; throat, chest, and sides of abdomen with small, round scattered dark spots."

Discussion: Besides the holotype (USNM 23993) and three topotypic paratypes (USNM 23994-96), nine additional specimens (AMNH 68229, 68271-68272, 68964-68968), (KU 28068) have been collected. The American Museum specimens are from the vicinity of Santa Bárbara, Chihuahua, Mexico. In the major distinctive characters these specimens fit perfectly the description of this subspecies. The length of the tail does not exceed the width of the head in any specimen by more than four millimeters; in two, its length is less than, and in two others equal to, the width of the head. The University of Kansas specimen was collected by Mr. Ray Alcorn on June 20, 1950, and arrived at the Natural History Museum on July 4, 1950. The color and color pattern were still clearly evident. The "reddish" color observed on the head of the type was present on this specimen and occurred also as the ground color of the dorsum of the body. The inner surface of the lips was a bright reddish orange. The scales of the abdomen appear to have been bright pink.

The Kansas University specimen was taken five miles north of Durango (city), Durango, Mexico, which suggests that Durango (city) was the place from which Doctor Palmer collected the type specimens. In view of this I restrict the type locality to Durango (city), Durango, Mexico.

Locality records: MEXICO. *Durango:* Durango 5 mi. N (KU 28068); no specific locality (USNM 23993-23996), (AMNH 1308). *Chihuahua:* Santa Bárbara (AMNH 68229, 68271-68272, 68964-68968).

Phrynosoma douglassii douglassii (Bell)

Agama douglassii Bell, Trans. Linn. Soc. London, vol. 16, 1828, (1833), pp. 105-107, pl. 10; Harlan, Med. and Phys. Researches, 1835, p. 141, fig. 3.

Phrynosoma douglassii Wagler, Natural Syst. Amph., 1830, p. 146; Gray, In Griffith's Cuvier's Animal Kingdom, vol. 9, 1831, p. 44; Wiegmann, Herpetologia Mexicana, 1834, p. 54; Duméril & Bibron, Érpétologie Générale ou Histoire Naturelle . . ., vol. 4, 1837, p. 323; Holbrook, North American Herpetology, 1 ed., vol. 3, 1838, p. 69, pl. 12, and *idem*, 2 ed., vol. 2, 1943, p. 101, pl. 14; Dekay, Zoology of New York, vol. 3, 1942, p. 31; Fitzinger, Systema Reptilium, 1843, p. 78; Gray, Catalogue of the Lizards in the British Museum of Natural History, 1845, p. 227; Duméril & Duméril, Catalogue Methodique de la Collection des Reptiles du Museum d'Histoire Naturelle, Paris, 1851, pp. 78-80; Cooper, Amer. Nat. vol. 3, 1869, p. 298; Hoffman, Amer. Nat. vol. 13, 1879, pp. 326-327; Boulenger, Catalogue of The Lizards

in the British Museum of Natural History, vol. 2, 1885, p. 240 (*part.*); Gentry, Proc. Acad. Nat. Sci. Philadelphia, 1885, p. 140 (*part.*); Stejneger, N. Amer. Fauna, no. 5, 1891, pp. 109-113; Van Denburgh, Occas. Papers California Acad. Sci., no. 5, 1897, p. 90 (*part.*); Van Denburgh, Proc. California Acad. Sci., ser. 4, vol. 3, 1912, p. 156 (*part.*); Stejneger & Barbour, Check List of the North American Amphibians and Reptiles, 1917, p. 59; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 11, 1921, pp. 40, 43; McLain, Critical Notes on a Collection of Reptiles from the West Coast of North America, 1899; Gadow, Proc. Zool. Soc. London, 1905, p. 213; Ditmars, Reptiles of the World, 1910, pp. 150-151.

Tapaya douglassii Girard, United States Exploring Expedition for the years 1838, 1839, 1840, 1841, 1842 under the Command of Charles Wilkes, USN. 1858, p. 398 (*part.*); Baird, Report of Exploration and Survey for a Rail Road Route from Sacramento Valley to the Columbia River, 1859; Baird, Report of the Pacific Rail Road Survey, vol. 12, 1860, p. 294; Cooper & Suckley, Report of the Pacific Rail Road Surveys, vol. 12, 1860, p. 294; Cooper & Suckley, Natural History of the Washington Territory, 1860, p. 294; Lord, Naturalist Vancouver Island, vol. 2, 1866, p. 302; Aug. Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 1, 1870, pl. 11, fig. 5, and Bocourt, *idem*, livr. 4, 1874, pp. 226-227, pl. 11, fig. 5a-5f.

Phrynosoma douglassii exilis Cope, Ann. Rept. U. S. Geol. Surv. Terrs., 1871, p. 468.

Phrynosoma douglassii douglassii Cope, Bull. U. S. Nat. Mus., no. 1, 1875, p. 49 (*part.*); Cope, Amer. Nat., vol. 13, 1879, p. 435; Cope, Report U. S. Nat. Mus., for 1898 (1900), p. 411, fig. 69 (*part.*); Dice, Univ. California Publ. Zool. vol. 16, 1916, pp. 300-301.

Phrynosoma douglassii pygmaea Yarrow, Proc. U. S. Nat. Mus., vol. 5, 1882, p. 443; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 70; Townsend, Proc. U. S. Nat. Mus., vol. 10, 1887, p. 238; Stejneger, N. Amer. Fauna, no. 3, 1890, pp. 112-113.

Phrynosoma douglassii hernandesi Cope, Ann. Report U. S. Nat. Mus. for 1898 (1900), p. 413 (*part.*).

Phrynosoma douglassii douglassii Bryant, Univ. California Publ. Zool., vol. 9, 1911, pp. 5, 22, pl. 3 (*part.*); Grinnell & Camp, Univ. California Publ. Zool., vol. 17, 1917, p. 164; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, 1922, pp. 368-377; Stejneger & Barbour, Check List of the North American Amphibians and Reptiles, 2 ed., 1923, p. 61; Erwin, The Eleventh Biennial Report of the Board of Trustees of the State Historical Society of Idaho, 1928, p. 32; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 67; Svihla & Svihla, Copeia, no. 1, 1933, p. 127; Gordon, Oregon St. Mono., Studies in Zool., no. 1, 1939, pp. 12, 15, 47-48, figs. 43, 44; Stejneger & Barbour Check List of North American Amphibians and Reptiles, 4 ed., 1939, p. 74; Graf, Jewett & Gordon, Copeia, no. 2, 1939, p. 103; Owen, Copeia, no. 3, 1940, p. 170; Anderson & Slater, Occas. Papers Dept. Biol. Coll. Puget Sound, no. 15, 1941, p. 111; Driver, Name That Animal, 1942, p. 348; Evender, Copeia, no. 4, 1946, p. 257.

Phrynosoma brevirostre Stone, Proc. Acad. Nat. Sci. Philadelphia, 1911, p. 229 (*part.*).

Phrynosoma orbiculare douglassii Klauber, Bull. Zool. Soc. San Diego, vol. 4, 1939, pp. 91-93; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 94.

Taxonomic history: The type description of this form was made by Bell (1829) from specimens in the British Museum, collected by Douglass in the Columbia River Area. Bell placed this animal in the genus *Agama*. The paper was read before the Linnean Society of London the same year, and published in volume 16 of the

Transactions of the Linnean Society of London in 1829. Wagler (1830) and Gray (1831) both placed it in *Phrynosoma*. Cope (1875) reduced it to subspecific rank, referring to it as *Phrynosoma douglassii douglassii*.

Diagnosis: Size small, rarely exceeding 125 mm.; occipital and temporal spines minute, projecting vertically; ground color generally dark brown or dark blue.

Description: Head broader than long; frontal area flat, covered with small, irregular, rugose scales; superciliary ridges distinct terminating posteriorly in a slightly enlarged blunt spine; nostrils small, on canthal line, separated by a distance equal to three and one-half to four times diameter of a single nostril; supralabials small, inconspicuous; infralabials small, increasing in size posteriorly to angle of jaw, continuous with postlabials; four postlabials, penultimate largest; chinshields only slightly enlarged, separated from infralabials by three small sublabials; gular scales subequal; two lateral neck patches of enlarged, soft spines borne on folds of skin, upper patch largest; occipital spines reduced to short vertical tubercles; interoccipital distance approximately three times basal diameter of spine; temporal shelf expanded, bearing several small, inconspicuous spines; dorsal scales of irregular size, largest keeled and set in a rosette of smaller, keeled scales; one row of soft spines in lateral abdominal fringe; tail short, covered with irregular scales; ventral scales smooth throughout; femoral pores 17-17, rows separated mesially by six preanal scales.

Dorsal ground color dark blue-gray; nuchal blotches black, indistinct; four pairs of dark brown to black spots on each side of back between neck and rump; spots usually outlined posteriorly in lighter color; one pair of spots on base of tail, four transverse bands on tail; head greenish gray with black flecks on tips of scales; ventral scales gray with scattered black flecks.

Variation: The chief variation in this subspecies is in the ground color, which ranges from dark gray to brownish or to dark yellow. The colors usually appear to be faded and are dull. The dorsal spots are usually edged posteriorly in a lighter color but in some individuals these blend with the ground color.

Discussion: This is one of the smallest forms of the species, rarely exceeding 70 mm. in snout-vent measurement. Specimens from the lava areas of Idaho tend to be much darker, often being dark gray or even black.

General distribution: This subspecies occurs in the northwestern part of the United States in the states of Washington, Oregon, Idaho and the northern parts of California and Nevada.

Locality records: Washington. *Kittitas Co.:* Ellensburg (Owen, 1940). *Okanogan Co.:* Pateros (Owen, 1940). *Pierce Co.:* Fort Steilcoon (USNM 9199); Puget Sound (USNM 217). *Sherman Co.:* Grant (Van Denburgh, 1897). *Spokane Co.:* (MVZ 43505-06). *Walla Walla Co.:* Walla Walla (USNM 10918, 5 spec.). *Whitman Co.:* Almota (Svihla & Svihla, 1933); Rock Lake (Svihla & Svihla, 1933). *Yakima Co.:* Selah (Owen, 1940); North Yakima (Van Denburgh, 1897).

Oregon. *Crook Co.:* Buck Creek (USNM 44974); Prineville (USNM 44907). *Deschutes Co.:* Deschutes (USNM 11473). *Gillian Co.:* Arlington (Gordon, 1939). *Harney Co.:* Burns (Gordon, 1939); Voltage (USNM 63264-65); Wagon Tire (Anderson & Slater, 1941). *Klamath Co.:* Klamath Falls (USNM 59288); Klamath Lake (Baird, 1859). *Lake Co.:* Chewauacan Valley, Olive (USNM 25911), between Warners and Goose Lakes (USNM 25912-13); Plush (USNM 25909-10), between Plush and Blue Creek (USNM 25925-33); Silver Lake Desert (MVZ 14990). *Linn Co.:* Sand Mountain (Graf, Jewett, & Gordon, 1939). *Morrow Co.:* Butler Creek, North Fork (Anderson & Slater, 1941); Heppner (USNM 44971-73). *Umatilla Co.:* Harmiston (Gordon, 1939); Holdman (Gordon, 1939); Cold Springs Landing, 5 mi. S (MVZ 16799). *Wasco Co.:* Antelope (USNM 45186).

California. *Modoc Co.:* Clear Lake (USNM 45138). *Siskiyou Co.:* Mount Shasta west base (USNM 12792, 2 spec.).

Idaho. *Ada Co.:* Boise (USNM 63266). *Bannock Co.:* Pocatello (USNM 48665). *Bingham Co.:* Aberdeen (UU 180, 177, 181); Blackfoot (USNM 16771); Fort Hall (Van Denburgh, 1922). *Butte Co.:* Big Butte (USNM 16772-73). *Butte* and *Custer Cos.:* Big Lost River (USNM 16318-19, 16774-75). *Cassia Co.:* Cottonwood Creek (McLain, 1899). *Elmore Co.:* Mountain Home (Evender, 1946). *Fremont Co.:* Elgin (BYU 8178). *Lemhi Co.:* Birch Creek, head of (USNM 16315-17). *Lincoln Co.:* Shoshone (McLain, 1899 listed as Logan Co.). *Madison Co.:* Rexburg (BYU 8054). *Nez Perce Co.:* Clearwater, 7 mi. above Lewiston (USNM 21473). *Owyhee Co.:* Little Owyhee River, 7 mi. N Nevada line (MVZ 24509-10), 10 mi. N Nevada line (MVZ 24517), 11 mi. N Nevada line (MVZ 24508).

NEVADA. *Elko Co.:* Bull Run Mountains (USNM 44816); Mountain City (Linsdale, 1940), 6 mi. S (Linsdale, 1940). *Humboldt Co.:* Martin Creek (Linsdale, 1940); Santa Rosa Mountains (Linsdale, 1940).

Phrynosoma douglassii hernandesi Girard

Phrynosoma orbiculare Hallowell, *in* Sitgreaves' Expedition down the Zuni and Colorado Rivers, 1863, p. 125, pls. 8, 9.

Tapaya hernandesi Girard, United States Exploring Expedition for the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, USN, vol. 20, Herpetology, 1858, p. 395. *Tapaya* used as a subgenus.

Tapaya hernandezii Baird, United States Mexican Boundary Survey, under the Order of Lieut. Col. W. H. Emory, Reptiles of the Boundary, vol. 2, 1859, p. 38; Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 4, 1874, p. 228.

Tapaya ornatissima Garman, Bull. Essex Inst. vol. 16-18, 1884.

Phrynosoma douglassii Cope, Proc. Acad. Nat. Sci. Philadelphia, 1866, p. 302; Coues, Report of the Geography and Geology of the Survey West of the 100th Meridian, under Lt. Wheeler, vol. 5, Zoology, 1875, p. 591 (*part.*); Cope, Proc. Acad. Nat. Sci. Philadelphia, 1883, p. 12; Boulenger, Catalogue of the Lizards in the British Museum of Natural History, vol. 2, 1885, p. 240, (*part.*); Gentry, Proc. Acad. Nat. Sci. Philadelphia, 1885, p. 140 (*part.*); Herrick, Terry & Herrick, Bull. Sci. Lab. Denison Univ., vol. 11, 1889, p. 134; Herrick, Terry & Herrick, Bull. Univ. New Mexico, vol. 1, 1899, p. 134, pl. 18, fig. 15; Lampe, Jahrb. Nassau. Ver. Naturk., vol. 64, 1911, p. 164; Eaton, Copeia, 1935, p. 151 (*part.*).

Phrynosoma hernandezii Cope, Bull. U. S. Nat. Mus., no. 1, 1875, p. 49; Yarrow, Report of the Geography and Geology of the Survey West of the 100th Meridian, under Lt. Wheeler, vol. 5, Zoology, 1875, p. 577; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 68 (*part.*); Cockerell, Amer. Nat. vol. 30, 1896, p. 227 (*part.*); McLain, Critical Notes on a Collection of Reptiles from the West Coast of North America, 1899, p. 8; Stone, Proc. Acad. Nat. Sci. Philadelphia, 1911, p. 229 (*part.*).

Phrynosoma douglassii ornatissimum Cope, Bull. U. S. Nat. Mus., no. 1, 1875, p. 49; Yarrow, Report of the Geography and Geology of the Surveys West of the 100th Meridian under Lt. Wheeler, vol. 5, Zoology, 1875, pp. 577-581 (*part.*); Cope, Report U. S. Nat. Mus. for 1898, (1900), p. 415, fig. 71 (*part.*); Strecker, Baylor Bull. vol. 18, 1915, p. 22; Weese, Biol. Bull., vol. 32, 1917, pp. 98-116.

Phrynosoma douglassii douglassii Yarrow, Report of the Geography and Geology of the Surveys West of the 100th Meridian, under Lt. Wheeler, vol. 5, Zoology 1875, p. 580 (*part.*); Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 68 (*part.*); Cope, Report U. S. Nat. Mus. for 1898, (1900), p. 111 (*part.*); Bryant, Univ. California Publ. Zool., vol. 9, 1911, p. 7.

Phrynosoma hernandesi Stejneger, N. Amer. Fauna, no. 3, 1890, p. 112, pl. 12, figs. 4a-c (*part.*); Van Denburgh, Proc. California Acad. Sci., ser. 2, vol. 6, 1896, p. 342; Stejneger, Proc. U. S. Nat. Mus., vol. 25, 1902, p. 151; Bailey, N. Amer. Fauna, no. 25, 1905, pp. 35, 43; Ruthven, Bull. Amer. Mus. Nat. Hist., vol. 23, 1907, pp. 542-544; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 3, 1913, pp. 397, 405; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 1917, p. 59 (*part.*); Van Denburgh, Occas. Papers California Acad. Sci., no. 10, vol. 1, 1922, pp. 382-385, pl. 31; Cuesta Terron, Ann. Inst. Biol., vol. 3, 1932, pp. 97-99; fig. 1; Little, Copeia, 1940, p. 263.

Phrynosoma douglassii hernandesi Cope, Report U. S. Nat. Mus. for 1898 (1900), p. 413, fig. 70 (*part.*); Stone & Rehn, Proc. Acad. Nat. Sci. Philadelphia, 1903, p. 32; Ditmars, The Reptile Book, 1907, p. 149, pl. 47, fig. 3 (*part.*); Strecker, Proc. Biol. Soc. Washington, vol. 21, 1908, pp. 165-166;

Ditmars, Reptiles of the World, 1910, pp. 150-151 (*part.*); Bryant, Univ. California Publ. Zool., vol. 9, 1911, p. 5; Ellis & Henderson, Univ. Colorado Studies, vol. 10, pp. 72-74, pl. 3, figs. 12, 14; Strecker, Baylor Bull., vol. 18, 1915, pp. 23-25; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 2 ed., 1923, pp. 61-62; Van Denburgh, Proc. California Acad. Sci., ser. 4, vol. 13, 1924, pp. 191-209; King, Copeia, 1932, p. 177; Mosauer, Occas. Papers Mus. Zool. Univ. Michigan, no. 246, 1932, p. 9; Burt, Amer. Midl. Nat., vol. 14, 1933, pp. 244-245; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, pp. 67-68; Smith, Trans. Kansas Acad. Sci., vol. 37, 1934, p. 287; McKee & Bogert, Copeia, 1934, p. 179; Burt, Amer. Midl. Nat., vol. 16, 1936, p. 324 (*part.*); Quaintance, Copeia, 1935, p. 184; Burt, Trans. Kansas Acad. Sci., vol. 38, 1936, p. 261; Gloyd, Bull. Chicago Acad. Sci., vol. 5, 1937, p. 113; Dodge, Bull. Grand Canyon Nat. Hist. Assoc., no. 9, 1938, pp. 31-33; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed., 1939, p. 73; Klauber, Bull. Zool. Soc. San Diego, no. 14, 1939, pp. 91-93; Tanner, Great Basin Nat., vol. 1, 1940, p. 141; Smith, Copeia, 1941, p. 114; Smith & Laufe, Trans. Kansas Acad. Sci., vol. 48, 1945, p. 338; Lowe, Herpetologia, 1947, p. 37; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, pp. 359-375; Bull. U. S. Nat. Mus., no. 199, 1950, p. 100.

Phrynosoma orbiculare hernandesi Klauber, Bull. Zool. Soc. San Diego, Bull. 14, 1939, pp. 91-93; Kauffeld, Amer. Midl. Nat., vol. 29, 1943, p. 345; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 94; Marr, Amer. Midl. Nat. vol. 32, 1944, p. 482.

Taxonomic history: This subspecies was first described by Girard (1858) as [*Phrynosoma*] (*Tapaya*) *hernandesi, Tapaya* being a subspecies under *Phrynosoma.* This actual combination does not appear, but it must be inferred. The specimens on which Girard based the description were not listed in his treatise. Stejneger (1890) designated USNM nos. 107 and 198 as the type specimens of Girard's *Tapaya hernandesi.* Inasmuch as the specimens bearing USNM no. 107 are of another species and since USNM no. 197 is listed on the Museum's type cards as the type specimen of *hernandesi,* I believe that USNM no. 107 as used in Stejneger's treatise is a misprint for number 197. Smith and Taylor (1950 a), believing that Stejneger's number 107 was intended for 197, have designated USNM no. 197 as the type specimen of *Phrynosoma douglassii hernandesi* and have restricted the type locality to Santa Fe, New Mexico. Actually the specimen bearing the tag no. 197 was collected by J. D. Graham and J. H. Clark in 1857, in Sonora. The tag bears no further data, but realizing that the Gadsden purchase was consummated in 1853 and that these men were with a Geological Survey Party, they must have been cognizant of the boundary. Therefore, I believe that "Sonora," as listed for no. 197, must be interpreted as the State of Sonora, Mexico. On the other hand, the tag bearing the USNM no. 198 and the locality Santa Fe, New Mexico, is loose in a jar with a specimen of *Phrynosoma douglassii hernandesi* which has attached to it a metal tag carrying the number 3034. Number 3034 must refer to some other collection,

since USNM no. 3034 is the type specimen of *Cnemidophorus gracilis.* Furthermore the specimen in the jar with the tag no. 198 agrees more closely with specimens of *Phrynosoma douglassii hernandesi* from southern Arizona, than it does with specimens of *Phrynosoma douglassii ornatissimum,* the only form positively known to occur at Santa Fe.

In view of the above facts I propose to regard USNM no. 197 as the type of *Phrynosoma douglassii hernandesi,* the type locality, however, being [the state of] Sonora, Mexico. When specimens are at hand from specific localities in northern Sonora, the locality should be restricted.

Diagnosis: Temporal spines long, each as long as, or longer than, its basal diameter; width of head at temporal region as wide as, or wider than, head at angle of jaws; dorsal spots bordered only posteriorly by light scales; tail more than one and one-half times width of head.

Description: Head broader than long; frontal area slightly concave, covered with small, irregular, rugose scales; superciliary ridges distinct, terminating posteriorly in triangular medium-sized spine; latter subequal in length to occipital spine; nostrils small, on canthal lines, separated by a distance equal to four or five times diameter of one nostril; nostrils entering from lateral surface of snout; supralabials small inconspicuous; infralabials increasing in size posteriorly; four postlabials markedly enlarged, continuous with infralabials; chinshields enlarged only slightly, separated from infralabials by a maximum of three sublabials; gular scales equal; two lateral neck patches of slightly enlarged flexible spines, lower patch reduced and joining upper patch at about its center; tympanum exposed; occipital shelf bearing several small tubercles; occipital spines small, widely separated usually directed posteriorly; interoccipital distance approximately three to three and one-half times basal diameter of one spine; temporal area expanded, extending lateroposteriorly; three temporal spines project posteriorly from posterior angle of temporal area; smallest temporal spine equal to, or larger than, occipital spine; lateral profile of temporal horns form straight line directed at first postlabial; dorsal scales small, imbricate, smooth, interrupted by numerous enlarged keeled scales; enlarged scales arranged in eight indistinct longitudinal rows, which decrease to four on rump and on the base of tail and to two on tail; one row of enlarged soft spines in lateral abdominal fringe; ventral

scales small, imbricate, smooth; femoral pores 15-16, rows separated mesially by three preanal scales.

Dorsal ground color gray; nuchal blotches brown to black; three pairs indistinct dark blotches spaced equally between neck and rump; blotches may alternate, several transverse bars on tail; head gray, temporal areas and spines cream, ventral scales cream with dark gray to black spots.

Variation: The texture of the dorsal scalation varies from a nearly uniformly smooth condition in specimens from southern Arizona to a rough bristly appearance in those from southern Utah. The distinctness of the dorsal pattern is variable, appearing as indistinct dark transverse bands without indication of a light posterior border or as somewhat distinct blotches with cresent shaped, light posterior borders. The blotches or bars may be either opposite or staggered in arrangement. The temporal areas of the head are usually of a color different from that of the remainder of the head, often being reddish or cream colored.

Discussion: This subspecies is most easily distinguished from *ornatissimum* by the character and color of the temporal area and spines. Any temporal spine of *hernandesi* is at least as long as the base is wide and often longer; they project posteriorly in uniform order. In *ornatissimum* the basal diameter nearly always exceeds the length of the spine. The spines in turn project upward in a somewhat irregular manner. In the latter form the width of the head at the angle of the jaws exceeds the width of the temporal area quite noticeably, whereas in *hernandesi* the width at the temporal area is equal to, and often exceeds, that at the angle of the jaws.

The dorsal pattern is quite characteristic in the two forms. The dorsal spots in *ornatissimum* are bordered both posteriorly and mesially in a light color; thus the spots are distinct whereas in *hernandesi,* at most, only the posterior limits of the spots are bordered and often there is no border at all.

Locality records: Arizona. *Cochise Co.*: Apache (USNM 8255-56, 8257, 8575); Fort Huachuca (USNM 42136, 22316, 17783-84, 19681-83, 32232-34, 18009, 21727); Lowell (USNM 8452, 5 spec., 8513); San Pedro River (USNM 21022-26). *Coconino Co.*: Grand Canyon (USNM 79686, 59838, 44629); Flagstaff (UU 207), (USNM 82000, 60173), (KU 383-85, 388-89, 381-83, 393); House Rock Station, 25 mi. S (KU 22231-35); House Rock Springs (USNM 44625), Kaibab Forest (UU 130-33, 197, 640, 459, 459a),

(USNM 79954, 71237-38); Little Colorado River (USNM 4599, 4580), Little Colorado Desert (USNM 15815); Painted Desert (USNM 15816-19); San Francisco Mountains (USNM 16198, 15802, 15799-814), (MVZ 8668, 6872, 8688); Stoneman Lake (USNM 59835); Tuba City, 1 mi. S (UU 1500, 6 spec. young); Williams (USNM 73748); Winona (USNM 60177-79). *Gila Co.*: Payson, 23 mi. E (KU 22230); Pine (BYU 2897, 2372-73), Roosevelt Reservoir (USNM 104287-91); White River Canyon (USNM 10191); no specific locality (KU 12934). *Graham Co.*: Mt. Trumbull (USNM 44636, 54610), 7 mi. N (USNM 44630-31); Stanley (MVZ 12885). *Maricopa Co.*: Cave Creek (KU 11302). *Mohave Co.*: Hualpai mountains (USNM 60184-7, 44624). *Navajo Co.*: Bubbling Spring Canyon (AMNH 2362); Kayenta (BYU 8016); March Pass Camp (UU 2170), (MVZ 2362). *Pima Co.*: Mount Lemon (KU 6965-66); Rincon Mountains (USNM 39311-12, 48549); Santa Catalina Mountains (USNM 47937), (MVZ 12878); Tucson (USNM 13968). *Pinal Co.*: Oracle, 6 mi. SE (Gloyd, 1937). *Yavapai Co.*: Camp Verde (USNM 24580-81); Fort Whipple (USNM 11858, 11857, 11862); Mingus Mountain (USNM 59836-37); Prescott (USNM 15738, 38555); 3 mi. N (KU 22799); Prescott National Park, Mt. Hope (KU 20150-55); Seligman (USNM 39048), 30 mi. E (MVZ 8689).

COLORADO. *Mesa Co.*: Mack (USNM 40142).

NEW MEXICO. *Grant Co.*: Gila National Forest (UU 176), (USNM 47084); no specific locality (KU 15517).

UTAH. *Carbon Co.*: Price (UU 1380, 1391, 1379, 1381), (BYU 8031). *Emery Co.*: Wellington 6 mi. S (UU 1385, 1387-90). *Garfield Co.*: Aquarius Plateau (BYU 599, 1920-22); Bryce Canyon Nat. Park (UU 1838), (BYU 8055); Henry Mt. (UU 302-5, 141); Table Cliff Mountains (BYU 201, 110-17); Widtose, 7 mi. E (MVZ 12875). *Iron Co.*: Cedar City, 5 mi. W (KU 20675); Parowan Mountains (USNM 45195-96). *Kane Co.*: Duck Creek (UU 1700-05, 1707-14); Orderville (BYU 2821, 2185), 15 mi. N (BYU 8050); Skink Valley (UU 1677-78). *San Juan Co.*: Blanding, 35 mi. NW (UU 2030); La Sal Mountains (BYU 8015, 8017); Monticello, 5 mi. W (UU 2888). *San Pete Co.*: Fairview (BYU 2859); Maple Canyon (UU 306a, 307). *Washington Co.*: Enterprise, west of (BYU 8056-57); Kolob Mountain (BYU 3103); St. George (UU 373); Zion Nat. Park (UU 375).

MEXICO. *Chihuahua*: Ramos (Smith & Taylor, 1950b).

Phrynosoma douglassii ornatissimum Girard

Phrynosoma douglassii Girard, *in* Stansbury's Exploration and Survey of the Valley of Great Salt Lake of Utah, 1852, p. 362, pl. 7 figs. 6-9 (*part.*); Cope, Ann. Rept. U. S. Geol. Surv. Terrs., 1871, p. 467; Coues, Report of the Geography and Geology of the Survey West of the 100th Meridian under Lt. Wheeler, vol. 5, 1875, p. 591 (*part.*); Gentry, Proc. Acad. Nat. Sci. Philadelphia, 1885, p. 140 (*part.*); Stejneger, N. Amer. Fauna, no. 5, 1891, p. 109; Van Denburgh, Bull. U. S. Fish Commission for 1894, p. 56; Van Denburgh, Occas. Papers California Acad. Sci., no. 5, 1897, p. 90 (*part.*); McLain, Critical Notes on a Collection of Reptiles from the West Coast of North America, 1899, p. 8; Van Denburgh, Proc. California Acad. Sci., ser. 4, vol. 3, 1912, p. 156 (*part.*); Van Denburgh, & Slevin, Proc. California Acad. Sci., ser. 4, vol. 5, no. 4, 1915, p. 105; Van Denburgh & Slevin, Proc. California Acad. Sci., ser. 4, vol. 11, 1912, pp. 28, 40, 43.

Tapaya ornatissima Girard, United States Exploring Expedition for the years 1838, 1839, 1840, 1841, 1842 under the Command of Charles Wilkes USN, vol. 20, Herpetology, 1858, p. 396; Baird, United States Mexican Boundary Survey, vol. 2, Reptiles of the Boundary 1859, p. 9; Baird, Report of the Exploration and Surveys to Ascertain the most Practicable and Economic Rail Route to the Pacific Ocean, vol. 10, Reports upon the Reptiles of the Route, 1859, p. 38; Aug. Duméril & Bocourt, Mission Scientifique au Mexique et dans l'Amérique, Études sur les Reptiles, livr. 1, 1870, pl. 11, fig. 6 and Bocourt, *idem*, livr. 4, 1874, p. 227.

Phrynosoma douglassii douglassii Cope, Bull. U. S. Nat. Mus., no. 1, 1875, p. 49 (*part.*); Coues, Report of the Geography and Geology of the Survey West of the 100th Meridian under Lt. Wheeler, vol. 5, 1875, p. 580 (*part.*); Coues & Yarrow, Bull. U. S. Geol. Surv., vol. 4, 1878, p. 285; Yarrow, Bull. U. S. Nat. Mus., no. 24, 1883, p. 68 (*part.*); Cope, Rept. U. S. Nat. Mus., for 1898, (1900), p. 411 (*part.*); Bryant, Univ. California Publ. Zool., vol. 9, 1911, pp. 5, 22, pl. 3 (*part.*); Pack, Copeia, no. 63, 1918, p. 91.

Phrynosoma douglassii ornatissimum Yarrow, Report of Geography and Geology of the Survey West of the 100th Meridian, under Lt. Wheeler, vol. 5, 1875, p. 581 (*part.*); Yarrow, Bull. U. S. Nat. Mus., no. 24, pp. 11, 69; Cope, Report U. S. Nat. Mus., for 1898, (1900), p. 415, fig. 71 (*part.*); Ditmars, The Reptile Book, 1907, p. 148; Bryant, Univ. California Publ. Zool., vol. 9, 1911, p. 5; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, 1922, vol. 1, pp. 377-380, pl. 30; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 2 ed., 1923, p. 62; Van Denburgh, Proc. California Acad. Sci., ser. 4, vol. 13, 1924, pp. 191-208; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 68 (*part.*); Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed., 1939, p. 74 (*part.*); Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1934, p. 94, (*part.*).

Phrynosoma hernandesi Stejneger, N. Amer. Fauna, no. 3, 1890, p. 112 (*part.*); Cockerell, Science, ser. 2, vol. 14, 1901, p. 111; Cockerell, Univ. Colorado Studies, vol. 7, 1910, p. 131; Ellis & Henderson, Univ. Colorado Studies, vol. 10, 1913, p. 72, pl. 3, figs. 12, 14; Ruthven & Gaige, Occas. Papers Mus. Zool. Univ. Michigan, no. 8, 1915, p. 23.

Phrynosoma ornatissimum Stejneger, N. Amer. Fauna, no. 3, 1890, p. 115, pl. 12, figs. 3a-3c; Cary, N. Amer. Fauna, no. 33, 1911, pp. 21, 23, 26; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 1917, p. 60.

Phrynosoma douglassii hernandesi Cope, Report U. S. Nat. Mus., 1898 (1900), p. 413 (*part.*); Richardson, Proc. U. S. Nat. Mus., vol. 48, 1915, p. 423; Burt, Amer. Midl. Nat. vol. 14, 1933, pp. 244-45 (*part.*).

Phrynosoma douglassii brevirostre Stone, Proc. Acad. Nat. Sci. Philadelphia, 1911, p. 229 (*part.*).

Phrynosoma hernandesi ornatissimum Ellis & Henderson, Univ. Colorado Bull., vol. 15, 1915, p. 260.

Phrynosoma hernandesi hernandesi Ellis & Henderson, Univ. Colorado Bull., vol. 15, 1915, p. 260.
Phrynosoma douglassii ornatum Stejneger, Copeia, no. 65, 1919, p. 3.
Phrynosoma orbiculare ornatissimum Klauber, Bull. Zool. Soc. San Diego, no. 14, 1939, p. 93.

Taxonomic history: Girard (1858) described this subspecies as [*Phrynosoma*] *Tapaya ornatissima* on the basis of specimens in the United States National Museum. He gave the distribution as the Eastern Mountainous regions of New Mexico, but did not designate a type specimen. Yarrow (1875) was first to reduce it to subspecific status, *Phrynosoma douglassii ornatissimum.* Stejneger (1890) designated United States National Museum No. 204 (2 specimens) as the types used by Girard in making his description. These specimens were collected in the Zuni Mountains, New Mexico, by Woodhouse.

Diagnosis: Tail longer than head width; temporal spines shorter than their basal diameter; head width at angle of jaw exceeding that at temporal area; dorsal dark spots bordered mesially and posteriorly by a narrow light band.

Description: Head markedly wider than long; frontal area concave, covered with medium-sized, irregular, rugose scales; superciliary ridges distinct, terminating posteriorly in a blunt triangular spine; nostrils on canthal lines, medium sized; internasal distance equal to three times diameter of single nostril; supralabials small, inconspicuous; infralabials small, increasing in size posteriorly; three enlarged postlabials continuous with infralabials; chinshields small, increasing in size posteriorly, separated from infralabials by three sublabials; gular scales equal; two lateral neck patches of enlarged soft spines; lower patch connecting to center of upper patch; tympanum exposed; occipital area with several small tubercles; occipital spines small, shorter than their basal diameter, projecting upward; interoccipital distance equal to about twice diameter of single spine; temporal shelf moderately expanded; temporal spines small, length less than their basal diameter; lateral profile of temporal spines a curved line projecting to snout; dorsal scales small, imbricate, with enlarged keeled scales forming eight indistinct longitudinal rows; these reduced to four on rump and base of tail, with two continuing on tail; one row of enlarged, soft spines in lateral fringe; ventral scales medium size, imbricate, smooth; femoral pores 17-17, rows separated by four preanal scales:

Dorsal ground color light brown; nuchal blotches dark brown to black; three pairs of dark brown to black spots evenly spaced

between neck and rump, members of second and third pairs alternating; all spots outlined mesially and posteriorly in light cream; several indistinct markings on tail; head light brown; ventral scales cream with black spots scattered throughout.

Variation: The occipital spines vary somewhat in size and to some extent in the angle at which they are attached to the skull. They are rarely horizontal in position. The ground color varies to fit the substratum upon which the animal lives. The pattern, however, is constant, varying only in intensity.

Discussion: See *P. d. hernandesi.*

Locality records: Arizona. *Apache Co.:* Adamona (USNM 82309), (MVZ 9014-15); Chin Lee (USNM 60172, 44626); Ganado, 4 mi. NW (USNM 44627); Mt. Baldy (USNM 118590); St. John, 6-8 mi. S (MVZ 9016-17, 9021-22, 9024-27); White Mountains (USNM 9637); Zuni River (USNM 3219). *Greenlee Co.:* Eagle Creek (Quaintance, 1935).

Colorado. *Archuleta Co.:* Pagosa (USNM 11964, 8443). *Costillo Co.:* Garland (USNM 8558).

New Mexico. *Bernalillo Co.:* Albuquerque (USNM 8451, 2 spec.), (MVZ 5359-61), (KU 11308); Albuquerque, San Pedro Mountains (USNM 58419-22); Albuquerque, 20 mi. E (USNM 201). *Catron Co.:* Glenwood, 5 mi. NE (MVZ 42575); Mogollon, 10 mi. N (KU 6546), 8 mi. W (KU 6544); Quemado (USNM 44701). *Colfax Co.:* Cimarron (USNM 22666). *Grant Co.:* Mimbres Mountains (USNM 47089); Silver Creek (MVZ 42571-72), 7 mi. N (MVZ 42573); Silver City (USNM 4849), (MVZ 42568), (KU 15516-18), 12 mi. W (MVZ 42574). *Lincoln Co.:* Ruidoso (USNM 32992). *McKinley Co.:* Fort Wingate (USNM 14408, 14396); Zuni Mountain (USNM 44566). *Otero Co.:* Cloudcroft (USNM 32990); Guadalupe Mountains (32983-84); Mescalero (USNM 25433, 25434); Mescalero Reservation (USNM 32991). *Rio Arriba Co.:* Canjilon Ranger Station (MVZ 25219); Espanola (USNM 44886); El Rito, 4 mi. N (KU 11303-04, 11300-01). *San Miguel Co.:* Pecos (USNM 32989); Sacramento Mts., Sapello Canyon (Stone & Rehn, 1903); no specific locality (USNM 199). *Santa Fe Co.:* Glorieta (USNM 32988); Ildefonso (USNM 8445); San Pedro (USNM 32985-7); Santa Fe (USNM 9635, 3 spec. 8449, 4866, 4785, 2 spec.) (KU 11305-07, 6976), 8 mi. SW (KU 11288-97); Santa Fe Canyon (USNM 90902). *Socorro Co.:* No specific locality (KU 6720-21). *Taos Co.:* Rio Colorado (USNM 8450); Taos (USNM 8515). *Valencia Co.:* Grants (USNM 44805); Inscription Rock

(KU 11298-99); San Mateo Peak (USNM 44569-70); Zuni Mountains (USNM 204); no specific locality (USNM 44702, 16000-01). *Torrance Co.:* Torrance (USNM 65832).

TEXAS. *El Paso Co.:* Guadalupe Mts. (Bailey, 1905); *Jeff Davis Co.:* No specific locality (Marr, 1944); Pecos River & Rio Grande (USNM 205).

Phrynosoma douglassii ornatum Girard

Phrynosoma ornatum Girard, Report of the Exploring Expedition for the years, 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, USN, vol. 20, 1858, Herpetology Atlas, pl. 21, figs. 1-5.

Tapaya douglassii Girard, Report of the Exploring Expedition for the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, USN, vol. 20, Herpetology, (in text), 1858, pp. 388-410 (*part.*); Baird, Report of the Exploration and Surveys to ascertain the most Practicable and Economic Rail Road Route to the Pacific Ocean, vol. 10, 1859, p. 18.

Phrynosoma douglassii Yarrow, Report of the Geography and Geology Surveys West of the 100th Merridian under Lt. Wheeler, vol. 5, 1875, pp. 580-581, 591-593 (*part.*); Van Denburgh & Slevin, Proc. California Acad. Sci., vol. 5, 1915, pp. 100, 105.

Phrynosoma douglassii ornatissimum Coues & Yarrow, Bull. U. S. Geol. & Geol. Surv., vol. 4, 1878, pp. 286-287, (*part.*); V. M. Tanner, Copeia, 1928, pp. 23-28; Ruthven, Occas. Papers Mus. Zool. Univ. Michigan, no. 243, 1932, p. 3. Stuart, Occas. Papers Mus. Zool. Univ. Michigan, no. 244, 1932, pp. 1-33, pls. 1-4; Knowlton & Janes, Copeia, 1934, p. 12, Knowlton & Thomas, Copeia, 1936, p. 65; Hardy, Proc. Utah Acad. Sci., Arts & Letters, vol. 15, 1938, p. 100; W. W. Tanner Proc. Utah Acad. Sci., Arts & Letters, vol. 16, 1939, p. 105; Linsdale, Proc. Amer. Acad. Arts & Sci., vol. 73, 1940, p. 232, map; W. W. Tanner, Great Basin Nat., vol. 1, 1940, p. 141.

Phrynosoma douglassii hernandesi Cope, Rept. U. S. Nat. Mus. for 1898 (1900) pp. 413-415 (*part.*); Richardson, Proc. U. S. Nat. Mus., vol. 48, 1915, pp. 405, 423-424.

Phrynosoma douglassii douglassii Pack, Copeia, 1918, pp. 91-92.

Phrynosoma douglassii ornatum Stejneger, Copeia, 1919, pp. 3-4; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 2 ed., 1923, p. 62; V. M. Tanner, Copeia, 1928, p. 23; Ruthven, Occas. Papers. Mus. Zool. Univ. Michigan, no. 243, 1932, p. 3; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 68; W. W. Tanner, Proc. Utah Acad. Sci., Arts & Letters, vol. 16, 1939, p. 105; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 4 ed., 1939, p. 74; W. W. Tanner, Great Basin Nat., vol. 1, 1940, p. 141.

Phrynosoma orbiculare ornatum Klauber, Bull. Zool. Soc. San Diego, no. 14, 1939, p. 93; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 95.

Taxonomic history: The name *Phrynosoma ornatum* first appears as a caption on a plate in the atlas accompanying Girard's work in the United States Exploring Expedition . . ., 1858. However, it was placed in the synonymy of *Tapaya douglassii* in the text of the same work. The explanation by Girard is that the plates were processed previous to the printing of the text and *ornatum* had been thought to be distinct and was so figured for the atlas. But it seems that he had changed his mind too late to correct the caption in the

atlas, but soon enough to correct the text. The name thus stands based on the figure in the atlas. Stejneger (1919) was first to clarify the use of the name.

Diagnosis: Temporal area as wide as, or wider than, head width at angle of jaws; length of each temporal and occipital spine equal to or greater than its basal diameter; light-colored borders generally confined to posterior portion of dorsal spots; size medium to small.

Description: Size medium to small; head wider than long; frontal area flat, covered with medium to large, irregular, rugose scales; snout moderately pointed; rostrofrontal angle obtuse; nostrils medium sized, slightly below canthal line, opening laterally; supralabials small, inconspicuous; infralabials small, increasing slightly in size posteriorly, continuous with postlabials; three enlarged postlabials extending from angle of jaw to postrictal scale; latter small, conical; chinshields small, increasing in size posteriorly, separated from infralabials by three small sublabials; gular scales subequal throughout; tympanum exposed, opening bordered anteriorly with several slightly enlarged scales; two lateral neck patches of enlarged soft spines; occipital area with several slightly enlarged tubercles; occipital spines short projecting slightly upward; basal diameter of each equaling its length; intraoccipital distance equal to approximately four times basal diameter of one spine; temporal area moderately expanded; three small temporal spines, length of each equal to, or greater than, its basal diameter; lateral profile of temporal horns forming straight line, projecting to approximate region of angle of jaw; dorsal scales small imbricate, smooth, interspersed with varying sizes of enlarged, keeled soft spines; larger scales forming from six to eight indefinite longitudinal rows between neck and rump, four rows on rump and base of tail, diminishing to two rows on tail; one row of enlarged soft spines in the lateral abdominal fringe; dorsal surface of legs with numerous enlarged keeled soft spines; arms with a few enlarged keeled scales anteriorly; ventral scales small, smooth, imbricate; femoral pores 12-14, rows separated mesially by three preanal scales.

Dorsal ground color greenish gray; nuchal blotches dark brown, fading into ground color ventrally and posteriorly; three pair dark brown or black dorsal spots between neck and rump; first spot near mid-point of above distance; dorsal spots bordered posteriorly in white; one pair dark spots on base of tail; several dark transverse bands on remainder of tail; head olive; horns light gray.

Variations: The proportions of the head and in particular the temporal area varies somewhat throughout the range of this subspecies. The temporal area is expanded and generally flattened above, similar to that of *hernandesi.* However, in some specimens this area may be slightly convex. The usual row of three small temporal spines may be augmented by a fourth spine.

The ground color may vary from a greenish gray to a light tan setting off dorsally the dark brown or black dorsal spots. The latter are usually bordered posteriorly in white or light gray, rarely being bordered mesially.

Discussion: This form is most closely related to *hernandesi,* differing in its smaller size, generally lighter color and the more moderate development of the temporal areas and spines. A major controversy has existed regarding the validity of this form, which I believe has been caused by a misunderstanding of the true relationships involved and a lack of an adequate picture of the species as a whole. The form is intermediate between *hernandesi* and *douglassii,* but has enough distinctive characters to warrant subspecific recognition.

General distribution: The range of this form coincides closely with the area covered by the old Pleistocene Lake Bonneville, extending from Iron County, Utah on the south, to southern Idaho on the north, and westward into the northeastern part of Nevada.

Locality records: NEVADA. *Elko Co.:* Carlin (USNM 45241); Deeth (Linsdale, 1940); 22 mi. N (Linsdale, 1940); Halleck (USNM 44819-21), 3 mi. S (USNM 71187).

UTAH. *Box Elder Co.:* Rosette, 8 mi. S (Knowlton & Janes, 1934); no specific locality (USNM 4927, 5321). *Cache Co.:* Hyrum (BYU 2809, 2118). *Millard Co.:* Filmore (Ruthven, 1932); Great Basin Experimental Station (BYU 433). *Salt Lake Co.:* Emigration Canyon (UU 1351, 2265); Ft. Douglas (UU 1968-70, 2306, 374), (BYU 2095, 2097, 2778); Little Black Mt. (UU 57, 56); Mill Creek Canyon (UU 2115); Salt Lake City (UU 8586, 3690), (USNM 60925, 318234, 60940-73, 42113, 4979); no specific locality (UU 125-129). *Tooele Co.:* Tooele Canyon (UU 205-06); Tooele Valley (UU 368). *Utah Co.:* Alpine (UU 369); Cedar Fort (USNM 44762-63); Lehi, west of (BYU 2786); Mt. Timpanogos (BYU 8051-52); Provo Bench (UU 371); Provo (BYU 3062, 3356); west side of Utah Lake (UU 2263).

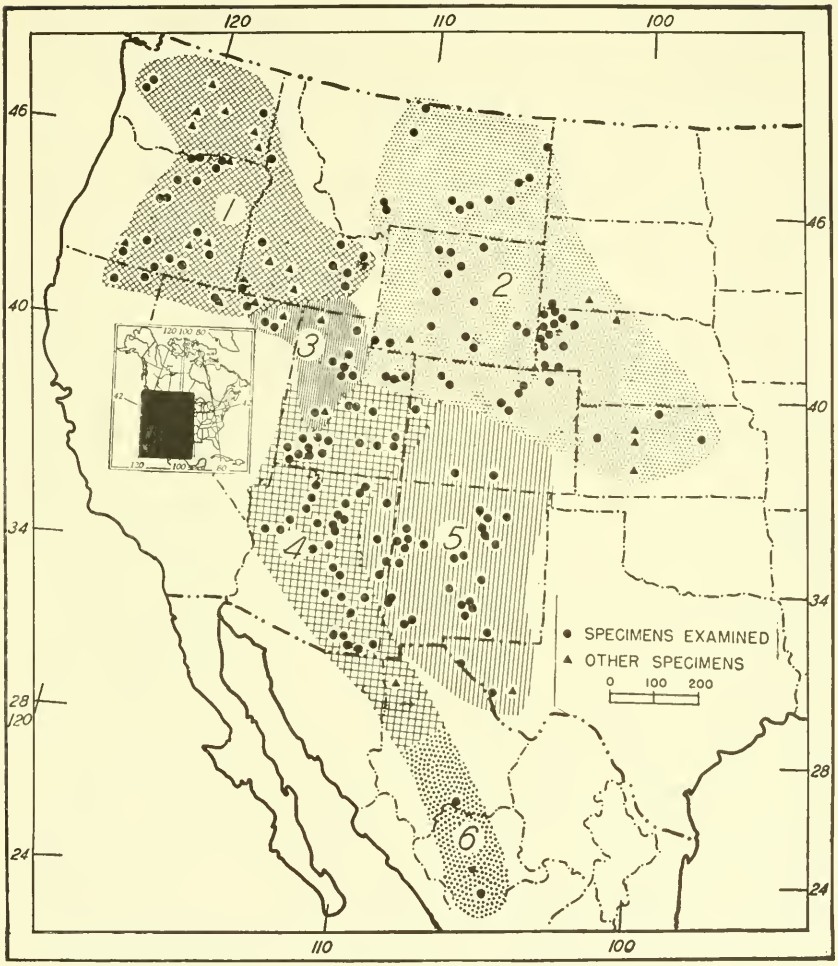

FIG. 10. Map showing the geographic distribution of the species *Phrynosoma douglassii*.

1. *Phrynosoma d. douglassii*
2. *Phrynosoma d. brevirostre*
3. *Phrynosoma d. ornatum*
4. *Phrynosoma d. hernandesi*
5. *Phrynosoma d. ornatissimum*
6. *Phrynosoma d. brachycercum*

Phrynosoma orbiculare cortezii Aug. Duméril and Bocourt

Phrynosoma orbiculare Wiegmann, Herpetologia Mexicana, 1834, p. 53, pl. 8, fig. 1; Blatchley, Proc. U. S. Nat. Mus., vol. 16, 1893, p. 41.

Tapaya cortezii Aug. Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 1, 1870, pl. 9, figs. 2, 2a-2g.

Tapaya orbicularis Var. A. Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études dans les Reptiles, livr. 4, 1874, pp. 223-224, pl. 11, figs. 2, 2a-2g.

Phrynosoma orbiculare cortezii Günther, Biologia Centrali-Americana, Reptilia and Batrachia, 1890, p. 78; Smith, Trans. Kansas Acad. Sci., vol. 37, 1934, pp. 291-292, pl. 11, fig. 1, pl. 12, fig. 6; Smith, Field Mus., Nat. Hist. Zool. Ser., vol. 24, 1939, p. 23; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, p. 349; Bull. U. S. Nat. Mus., no. 199, 1950, p. 98.

Diagnosis: This form can be separated from the others of the species by greater head width to head length ratio; temporal horns projecting farther posteriorly than occipitals; rarely more than a single series of preanal pores.

Description: Head considerably broader than long; frontal area flat; nares on canthal line, separated by distance equal to two times diameter of naris; superciliary spine approximately one half length of occipitals, concave on outward side, terminating the moderately developed superciliary ridges; a series of five enlarged tubercles anterior to occipital spines; latter approximately as broad as long, interoccipital space equaling about one half spine diameter; three temporal spines present, innermost longer than broad and projecting slightly beyond occipitals; space between occipital spine and innermost temporal spine approximately equal to basal diameter of innermost temporal; temporal shelf covered with moderately enlarged scales; supralabials 7-9, small, enlarging posteriorly; infralabials 8-9, last four becoming pointed; postlabials three, the row curving downward coming in contact with postrictal at anterioventral corner of exposed tympanum; sublabials moderately large, separated from infralabials by three small scales; gular scales subequal throughout; lateral neck fold having five enlarged spines, second smaller fold more ventral, bearing four spines; a single mid-dorsal nuchal spine; vertebral row of minute scales bordered by series of slightly enlarged keeled scales; three series of large soft spines forming longitudinal rows down either side of back, two inner rows of each side converging into one at base of tail and continuing on tail as single row; single series of lateral abdominal spines; corresponding series on tail; dorsal femoral area with three indistinct spine rows; fringes on anterior upper arm and posterior surface of lower area; ventral scales smooth throughout; femoral pores 15-16, separated mesially by four preanal scales.

Dorsum of head uniformly blackish brown; ground color of dorsum of body ivory, darkening laterally and posteriorly into dark gray nuchal blotches black, separated mesially by normal ground color; four pairs of indistinct dark patches each edged posteriorly in light ground color, paralleling vertebral column; several indistinct spots on tail; ventral ground color white, with narrow irregu-

lar black lines forming reticular network; tail with alternating spots anteriorly, transverse bands toward end.

Variation: A series of some 30 specimens from Las Vigas, Veracruz, and vicinity, show the following major variations:

The femoral pores in this subspecies usually are arranged in a single row. However, in five of the specimens extra pores were present forming an incomplete second row on the preanal area, posterior to the main row. The characteristic narrow reticulate ventral pattern appears markedly wider and darker in several specimens, being almost totally black in one. In most adults the occipital spines project farther posteriorly than the temporal spines; otherwise, the two sets of spines of adults were of equal length.

Locality records: Mexico. *Puebla*: Atzitzintla (Smith, 1939); San Diego, south of Tehuacán (Smith & Taylor, 1950); San Marcos, 15 mi. E (EHT-HMS 1845). *Veracruz*: Jalapa (USNM 4596, 3 spec.); La Joya, 1 mi. W (EHT-HMS 28861-62); Limón, 3 km W (KU 25882); Las Vigas (KU 25852, 25854-56, 25858-61, 25863-64, 25866-73, 25875-81, 25883-86); 4 km E (KU 25874); 5 km E (Smith & Laufe, 1945); Perote (Smith & Taylor, 1950b); San Andrés, South of (Blatchley, 1893); Zacualpillo, 6 km WSW (KU 25853, 25857, 25862, 25865).

Phrynosoma orbiculare dugesii Aug. Duméril & Bocourt

Tapaya Dugesii Aug. Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 1, 1870, pl. 11, figs. 3a-3g. (They state that *Tapaya* is a subgenus under *Phrynosoma*.)

Tapaya orbicularis Var. B. Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr. 4, 1875, pp. 224-225, pl. 11, fig. 3, 3a-3f.

Phrynosoma orbiculare (var.) *dugesii* Boulenger, Catalogue of the Lizards in the British Museum of Natural History, vol. 2, 1885, p. 243; Günther, Biologia Centrali-Americana, Reptilia and Batrachia, 1890, p. 78.

Taxonomic history: August Duméril and Bocourt (1870) named this form from two specimens collected at Colima, Mexico, by Alfredo Dugès. It was given full specific rank. Bocourt (1874) reduced it to variety β under *Tapaya orbicularis*. Boulenger (1885) correctly referred it to *Phrynosoma orbiculare* (var.) *dugesii*.

Diagnosis: This rare form can be recognized by the approximately equal extension posteriorly of occipital and temporal horns; by head being nearly as long as wide; and by fewer (14-14) femoral pores all in single row on each side.

Only the type specimens (not seen by me) are known. Bocourt's (1874) description follows:

"Tête relativement déprimée; sa longueur, comprise entre le bout du museau et l'extrémité d'une des épine de l'occiput, égale sa plus grande largeur; écailles sous-labiales postérieures pointues, plus grandes que les scutelles inframaxillaries; ces denières, de forme rectangulaire, sont disposées en une rangée sous chacune des branches de la mâchoire inférieur; une squame conique et pyramidale à la commissure des lèvres; narines percées à l'extrémité antérieure de la ligne sourcilière; plaque occipitale ovalaire, plus grande que les tubercles nombreux qu'elle précède; treize à quinze pores sur la partie interne des cuisses; queue entrant pour les deux cinquièmes dans la longueur totale de l'animal, charactérisée, chez les mâles, par une basé volumineuse et par deux écailles postanales distinctement plus grandes que les autres; une seule dentelure sur la périphérie de l'abdomen, formée de trente squames trièdres et subpyramidales; une autre squame de même forme au-dessus de chacun des bras; longueur du tibia égalant le distance comprise entre le bout du museau et la naissance de épines occipitales; écailles du ventre, de la gorge et du dessous de la queue lisses.

"*Coloration.* Teinte générale roussâtre; chacun des côtés du cou marqué d'une grande tache noire; à droite et à gauche de la ligne vertébrale, une double série de trois autres taches brunes, circonscrites en arrière par un étroit filet jaune; membres, bassin et queue traversés par des bandes de même couleur; tempes et épines céphaliques d'un rouge brique. En dessous, sur un fond jaunâtre, se détachent des marbrures ou taches noires confluentes, répandues sur le ventre et sur la queue; une ligne de cette dernière teinte parcourt la région médio-abdominale."

General distribution: Known only from Colima.

Locality record: MEXICO. *Colima:* No specific locality (Aug. Duméril & Bocourt, 1870).

Phrynosoma orbiculare orbiculare (Linnaeus)

Tapayaxin Lacertus orbicularis Hernandez, Plantos Animales de las Nueva España . . ., libr. 9, c. 16, 1651, p. 327, fig. (unnumbered).
Lacerta orbicularis spinosus Seba, Locupletissimi Rerum Naturalium Thesauri accurati Descriptio, et Iconibus Artificiosissimis Expressio, Per Universan Physices Historiam, vol. 1, 1734, p. 141, pl. 83, figs. 1-2.
Lacerta orbicularis Linnaeus, Systema Naturae, ed. 12, 1766, p. 365 (*part.*).
Cordylus orbicularis Laurenti, Specimen Medicum, Exhibens Synopsin Reptilium . . ., 1768, p. 55.
Tapaja orbicularis *Oken, Lehrbuch der Naturgeschichte dritter Theil. Zoologie zweite Abteilung. Fleischthiere. Jena, 16, 1816, p. 294.
Tapayis orbicularis Gray, Ann. Philos., NS vol. 26, 1825, p. 197.

* Oken used *Tapaja* in a subgeneric sense, under the genus *Agama*. The trivial names of *Tapaja* are not used with it, but with *Agama*.

Tapaya orbicularis Fitzinger, Neu Classification der Reptilien, 1826, p. 17; Girard, Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, USN., vol. 20, Herpetology, 1858, p. 406; Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, Études sur les Reptiles, livr., 4, 1874, pp. 221-222, pl. 11, figs. 1-1a-g.

Phrynosoma orbiculare Wiegmann, Isis von Oken, vol. 21, 1828, pp. 365-369; Gravenhorst, Act. Acd. Caes. Leopold. Carol. Nat. Cur., vol. 16, pt. 2, 1833, p. 912, pl. 62; Wiegmann, Herpetologia Mexicana, 1834, p. 53; Duméril & Bibron, Erpétologie Générale au Histoire Naturalle, des Reptiles, vol. 5, 1837, pp. 321-323; Gray, Catalogue of the Species of Lizards in the Collection of the British Museum of Natural History, 1845, p. 228; Duméril & Duméril, Catalogue Methodique de la Collection des Reptiles du Muséum d'Histoire Naturelle de Paris, 1851, pp. 78-80; Girard, in Stansbury's Exploration of the Valley of the Great Salt Lake of Utah, 1852, p. 359; Sumichrast, Arch. Sci., Phys. Math., vol. 19, 1864, p. 60; Garman, Biol. Essex Inst. vol. 19, 1887, p. 131; Cope, Rept. U. S. Nat. Mus., 1898 (1900), pp. 407, 417-419 (*part.*); Gadow, Proc. Zool. Soc. London, 1905, p. 213; Ditmars, Reptiles of the World, 1910, pp. 150-151, 153; Ruthling, Copeia, no. 72, 1919, pp. 67-68; Mertens & Wolterstorff, Abhandl. Ber. Mus. Natur. Heimatk. Natur. ver. Magdeburg, vol. 6, pt. 2; 1930, p. 158; Ochoterena, Ann. Inst. Biol., vol. 3, 1932, pp. 81-94; Dunn, Proc. Acad. Nat. Sci. Philadelphia, vol. 88, 1936, p. 475.

Agama orbiculare Bell, Trans. Linn. Soc. London, vol. 16, 1829, pp. 105-107.

Phrynosoma Wiegmanni Gray, Zoology Beechy's Voyage, 1839, p. 96.

Tapaya orbicularis longicaudatus Dugès, La Naturalieza, ser. 2, vol. 1, 1888, p. 177.

Phrynosoma orbiculare orbiculare Günther, Biologia Centrali-Americana, 1890, p. 78; Smith, Trans. Kansas Acad. Sci. vol. 37, 1934, pp. 287-297, pl. 11, fig. 2 and pl. 12, fig. 5; Smith, Ann. Carnegie Mus., vol. 27, 1939, p. 315; Taylor & Knobloch, Proc. Biol. Soc. Washington, vol. 53, 1940, pp. 125-126; Smith & Necker, Anales de la Escuela Nacional de Ciéncias Biologicas, vol. 3, 1943, pp. 216-218, pl. 2, fig. 1; Smith & Laufe, Trans. Kansas Acad. Sci., vol. 48, 1945, pp. 336-337; Smith & Taylor, Univ. Kansas Sci. Bull. vol. 33, pt. 2, 1950, pp. 329, 375; Bull. U. S. Nat. Mus., no. 199, 1950, pp. 97-98.

Taxonomic history: The unnumbered figures of Hernandez (1615) as copied by Seba (1734) formed the basis of the Linnean designation *Lacerta orbicularis.* Laurenti (1768) removed it from *Lacerta* and placed it in his genus *Cordylus.* The two species *hispidus* and *orbicularis,* which he placed in this genus were both based upon the figures of Seba (*op. cit.*). The former was based on plate 109, fig. 6, and the latter upon plate 83, figs. 1, 2, which in turn were reproduced from Hernandez. Oken (1816) relegated *orbiculare* to his subgenus *Tapaja* under the genus *Agama.* Gray (1825) placed *orbiculare* in his subgenus *Tapayia* and was followed by Fitzinger (1826) who assigned it to *Tapaya.* All three names antedate Wiegmann's (1828) *Phrynosoma orbiculare.* Aug. Duméril and Bocourt (1870) Bocourt (1874) and Girard (1858 referred *orbiculare* to *Tapaya.* Günther (1890) correctly used the name *Phrynosoma orbiculare* variety *orbiculare* and this has, in general, been followed since.

Diagnosis: This Mexican Plateau form can be recognized by: head only slightly wider than long; occipital spines projecting

backwards beyond temporal spines; additional preanal pores usually forming a double series mesially.

Description: Head slightly broader than long; nares on canthal line, separated by distance equal to approximately twice diameter of one naris; temporal spines nearly equal in size to, and projecting back to a point slightly less than occipital spines; distance between base of occipital spines less than basal diameter of one spine; short inconspicuous interoccipital spine present; three enlarged temporal spines, inner one largest; two tubercles on occipital shelf in front of occipital spines; supralabials 9-10, rounded on ventral surface; infralabials slightly enlarged 8-8, three pointed postlabials forming modified fringe at the angle of the mouth; long, broadly based postrictal at anterioventral corner of auricle; chinshields moderate in size, extending from small mental to below enlarged postlabials; three small sublabials separating chinchields from infralabials; gulars subequal; gular fold large; abdominal scales smooth throughout, 38-40 across widest part of abdomen; femoral pores 14-15; rows separated mesially by five preanal scales; extra pores forming double row on preanal area; several indistinct rows of enlarged scales on back converging into two paired rows on rump; two rows of spines on tail; single row of lateral abdominal spines extending from shoulder above arm to groin.

Dorsal ground color yellowish tan with brown and grayish-brown blotches; nuchal blotches dark, extending to above shoulders; three pair smaller less conspicuous dark spots over remainder of back; tail traversed by several dark bands; ventral surface of body with dark, heavy, reticular pattern that nearly obliterates light ground color; tail with several dark bands corresponding to those on dorsal surface.

Variation: The head proportions in this form vary from a condition in which the head is equal in length and width to a condition in which the head is 22 percent wider than long. There are often additional femoral or preanal pores which make a double row usually in the preanal area. The ventral pattern usually consists of a network of broad, dark bands, however, a light-spotted condition may occur. The occipital spines project posteriorly beyond the temporal spines in nearly all adult specimens.

Discussion: The conspecificity of the species *P. orbiculare* and *P. douglassii* proposed by some authors has been found to be erroneous. The two are undoubtedly distinct species.

General distribution: The distribution of this form is on the plateau of Mexico from Chihuahua and Nuevo León, south to Morelos and Puebla.

Locality records: MEXICO. *Chihuahua:* Chihuahua City, S of (Smith & Taylor, 1950b); Minaca, 21 mi. S (Dunn, 1936); Mojárachic (EHT-HMS 23046-47, 30125); Samachique (Smith & Taylor, 1950). *Distrito Federal:* Navitas, between Chalco and (Smith & Taylor, 1950); Tacuila, 3 mi. W (AMNH 15423-24); Tlalpam (Smith & Taylor, 1950); Tlalenpantla (Smith & Taylor, 1950). *Durango:* Ciudad (Günther, 1890); Coyotes (Smith, 1939); El

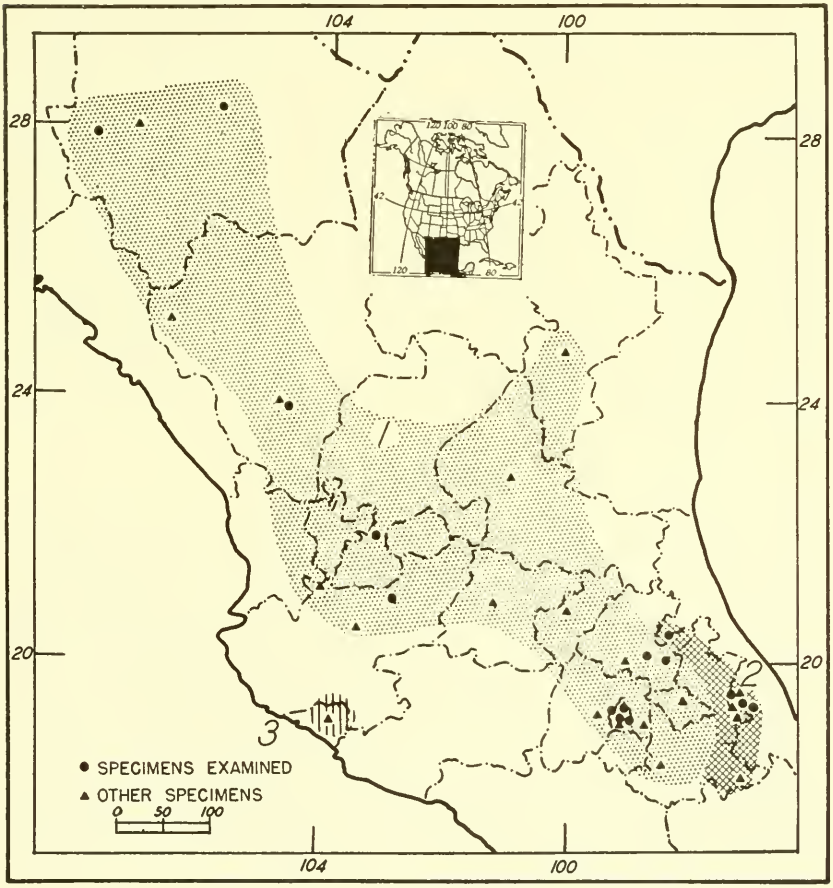

FIG. 11. Map showing the geographic distribution of the species *Phrynosoma orbiculare*.

1. *Phrynosoma o. orbiculare* 2. *Phrynosoma o. cortezii*
3. *Phrynosoma o. dugesii*

Salto (USNM 47469), 10 mi. E (AMNH 68359). *Guanajuato:* Guanajuato (city) (Smith & Taylor, 1950). *Hidalgo:* Actopan (Smith & Taylor, 1950); El Chico Parque Nacional (EHT-HMS 19235); Mexico (city), 65 km. N (EHT-HMS 19240, 23985); Pachuca, near (EHT-HMS 22245); Tulancingo, 2-3 mi. W (EHT-HMS 19237-38). *Jalisco:* Río Santiago, north of (Günther, 1890); Guadalajara (Smith & Taylor, 1950); Balaños (Smith & Taylor, 1950b); Yahualica, 2 mi. W (KU 28067). *Michoacán:* Jorullo, above Zumpango (Smith & Taylor, 1950b). *Morelos:* Tres Marías, near km. 57 (Smith, 1934); *Nuevo León:* Hacienda Pablillo, above Galeana (Dunn, 1936). *Puebla:* Matamoros (Smith & Taylor, 1950); Rió Otlati (Smith & Laufe, 1945); San Martín (USNM 47706), 15 km. NW (Smith & Laufe, 1945); Tezuitlán (Smith & Taylor, 1950); Tlalnepantla (Smith & Taylor, 1950). *Querétaro:* No specific locality (Smith & Taylor, 1950). *San Luis Potosí:* San Pedro (Dunn, 1936); Sapotillo (AMNH 69702). *Mexico:* Dos Rios (EHT-HMS 31627); Lerma (Smith & Taylor, 1950); Mexico City (USNM 12717), 17 km. ESE (Smith & Laufe, 1945), 23 km. SE (Smith & Laufe, 1945); San Andres (Smith & Taylor, 1950); San Barlolito, 1 mi. W (AMNH 15426-28); El Tajo de Tequisquiac (MVZ 8844-49); Tiza, 45 km. N Mexico City (EHT-HMS 10448). *Tlaxcala:* Tlaxcala City, 13 km. NE (Smith & Laufe, 1945). *Zacatecas:* Plateado (USNM 47874, 47876-78); Sierra Madre Mts. (Taylor & Knobloch, 1940).

Phrynosoma ditmarsi Stejneger

Phrynosoma ditmarsi Stejneger, Proc. U. S. Nat. Mus., vol. 29, 1906, pp. 565-567; Ditmars, The Reptile Book, 1907, p. 154, pl. 46, figs. 3, 7, 48; Reptiles of the World, 1910, p. 150; Lampe, Jarhb. Nassau Ver. Naturk., vol. 64, 1911, p. 163; Bryant, Univ. California Publ. Zool., vol. 9, 1911, p. 5; Stejneger & Barbour, Check List of the North American Amphibians and Reptiles, 1917, p. 58; Van Denburgh, Occas. Papers California Acad. Sci., no. 10, 1922, pp. 386-387; Stejneger & Barbour, Check List of the North American Amphibians and Reptiles, 2 ed., 1923, p. 61; Cuesta Terron, Anal. Inst. Biol. vol. 3, 1932, pp. 99-100, fig. 2; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, 3 ed., 1933, p. 67; Smith, Trans. Kansas Acad. Sci., vol. 37, 1934, p. 287; Stejneger & Barbour, Check List of North American Amphibians and Reptiles, ed. 4, 1939, p. 73; Burt, Trans. Kansas Acad. Sci., vol. 38, 1936, pp. 261-300, 304; Stejneger & Barbour, Bull. Mus. Comp. Zool. Harvard Coll., vol. 93, 1943, p. 93; Bogert & Oliver, Bull. Amer. Mus. Nat. Hist., vol. 83, 1945, pp. 315, 319, 334; Smith & Laufe, Trans. Kansas Acad. Sci., vol. 48, 1945, p. 337; Smith, Handbook of Lizards, 1946, pp. 289, 297-299.

Taxonomic history: The species *Phrynosoma ditmarsi* was described and named by Stejneger (1906) from two specimens given to the United States National Museum by Raymond Ditmars. The

specimens were collected by Mr. Eustace in northern Sonora, Mexico and sent to the New York Zoological Society where they were kept alive for some time. The validity of this species has never been questioned.

Diagnosis: This rare species can be distinguished by the following characters: nostrils on canthal line; one series of serrate scales bordering abdomen; tympanum exposed; single enlarged row of scales on gular area; ventral scales keeled throughout; lower jaw greatly expanded; five to seven sublabial scales; characteristic "horns" absent.

Stejneger's original description (1906:565-567) based on the holotype, an adult male, is as follows:

"Head much broader than long; nostrils in the line of canthus rostralis; tympanum entirely posterior, vertical to the axis of the body, concealed in the anterior neck fold, naked; no horns, the scales which in the other species form more or less projecting spines being only low bosses or protuberances; the postocular boss, a broad triangular pyramid, its three edges being continuations of the superciliary, the supraocular, and the orbito-temporal ridges; an abrupt raised orbito-temporal ridge from tip of postorbital boss to outer edge of the supratemporal expansion at the base of the scale corresponding to the outer temporal horn in other species, two scales corresponding to temporal horns slightly enlarged, depressed, the posterior, or inner, slightly pointed; below the scale row forming the upper posterior edge of the supratemporal expansion on each side a small conical spine; supratemporal expansion very wide, nearly straight behind, with a very deep and narrow occipital notch; no temporal ridge; on the edge of the fold in front of the ear a vertical series of 4 small spines; rostral very low; supralabials very small, scarcely differentiated from the scale row above, about 15 in number; about 15 small lower labials, the posterior ones gradually increasing in size, though not larger than the scutes forming the orbito-temporal ridge, and with a raised keel; a small spine behind the last lower labial, separated from it by a single scale; along the edge of the lower mandible a series of enlarged, strongly keeled submandibulars, increasing in size backward, the keels of the posterior ones slightly produced and pointed behind; mandible exceedingly deep, the distance between angle of mouth and base of submandibular shields being greater than the diameter of the orbit; large flat space between the lower labials and the submandibulars covered with polygonal scales of varying sizes, similar to those covering the upper surface of the head, about 5 in

a row; all head scales keeled and wrinkled; gular scales small, keeled; a series of spines on each side of the posterior half of the throat near the submandibulars and parallel with them; gular fold with transverse series of spines and a few isolated clusters of spines; a very heavy angular fold on each side of the neck, both the vertical and horizontal portion armored with clusters of large spines; back and upper surfaces of hind legs and tail with scattered larger, bluntly keeled scales, the largest with their base surrounded by a "rosette" of smaller scales, which are larger than those forming the general dorsal lepidosis; a single series of marginal scales, which are enlarged and bluntly pyramidal, set between 2 basal rows of slightly enlarged scales; scales of the fore legs and lower surfaces strongly keeled, the former pointed behind; a series of 13 (14) femoral pores on each side, separated on the middle of the belly by 4 scales, the pores piercing the scales near the posterior margin; base of tail strongly swollen, with 2 enlarged postanals; tail once and a third longer than head.

"Color (in life) 'reddish—the color of dry building sand, with very obscure markings,' according to Mr. Ditmars; in alcohol, pale yellowish gray, with two faint, narrow, brownish bands across the lower back; underside whitish, with very obscure dusky spots."

Discussion: Three specimens of this species are now known. Two are in the collection of the U. S. National Museum and the third in the American Museum of Natural History. The latter specimen carries only the general locality data of northern Sonora and thus adds nothing to our knowledge of the geographic distribution of the species. The absence of the spines, the enormous development of the lower jaw, the extreme notched condition of the occipital area and other cranial features would seem to indicate that the nearest relative of *P. ditmarsi* is *douglassii.* This affinity is however, by no means close for numerous characters will adequately separate the two.

Distribution: This species has been reported only from the general locality of northern Sonora.

Locality records: MEXICO. *Sonora*: Near boundary of Arizona (USNM 36022, 36012); northern Sonora (AMNH 557).

Phrynosoma boucardii Aug. Duméril and Bocourt

Tapaya boucardii Aug. Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale; Études sur les Reptiles, livr. 1, 1870, pl. 11, figs. 4a-f; and Bocourt *idem*, livr. 4, 1874, pp. 225-226, pl. 11, fig. 4, 4a-f.

Phrynosoma boucardii Boulenger, Catalogue of the Lizards in the British Museum of Natural History, 2 ed., vol. 2, 1885, p. 234; Herrick, Terry & Herrick, Bull. Sci. Lab. Denison Univ., vol. 11, 1889, p. 133; Cope, Rept. U. S. Nat.

Mus. 1898 (1900), p. 407; Bryant, Univ. California Publ. Zool., vol. 9, 1911, p. 5; Smith & Laufe, Trans. Kansas Acad. Sci., vol. 48, 1945, p. 338; Smith, Journ. Washington Acad. Sci., vol. 39, 1949, p. 38; Smith & Taylor, Univ. Kansas Sci. Bull., vol. 33, pt. 2, 1950, p. 333; Bull. U. S. Nat. Mus., no. 199, 1950, pp. 98, 99.

Taxonomic history: Aug. Duméril and Bocourt (1870) described and named this species from specimens in the Museum d'Histoire Naturelle de Paris, collected by M. Boucard on the plateau of Mexico. They placed the species in the subgenus *Tapaya.* Boulenger (1885) discarded the subgenus *Tapaya,* placing it in *Phrynosoma* where it has since remained.

Diagnosis: Nostrils on canthal line; one row of lateral abdominal scales; gular scales subequal and faintly keeled; superciliary spines large and prominent.

Description: Head broader than long, distinctly triangular; frontal area inclined steeply forward; nostrils on canthal line, of moderate size; space separating nostrils approximately two and one-half to three times diameter of nostril; superciliary ridges slightly raised, ending posteriorly in a large semicircular spine oriented with flat or concave side laterad; occipital spines moderately long and divergent; interoccipital space greater than basal diameter of one occipital spine; temporal shelf moderately expanded, edged laterally with three temporal spines, posterior one being only slightly smaller than occipital spine; tympanum exposed; infralabials increasing in size posteriorly and continuous with postlabials; latter curving slightly downward to meet chinshields immediately in front of long conical postrictal spine; three small sublabials separating chinshields from infralabials; gular scales subequal, imbricate, pointed posteriorly, and lightly keeled; gular fold covered posteriorly by minute scales; large prescapular fold bearing series of large pointed spines projecting from neck posterior to tympanum; second smaller fold appearing just below, and more or less connected to above; single lateral abdominal scale row borne anteriorly on fold of skin, originating in front of arm attachment, extending to near mid-point of body where fold disappears; dorsal squamation consisting of vertebral line of small imbricate scales bordered on either side by row of slightly larger keeled scales; six indistinct, longitudinal rows of enlarged spines; two rows continuing on tail; neck bearing pair of large dorsolateral spines; ventral scales smooth throughout; eight or nine femoral pores on each side, rows being separated mesially by five preanal scales.

Dorsal ground color light tan to gray; pair of dark brown to black

neck blotches extending from posterior limits of head laterally over shoulder area to neck folds, followed by three pairs of dark brown spots each surrounding large dorsal spine; dark area on base of tail, followed by approximately six transverse bands on tail; head olive with three faint vertical bars below eye; ventral color pale yellow with numerous black spots, some of which unite to form reticular pattern.

Distribution: This species has been reported only from the Mexican states of Guanajuato and Hidalgo. Probably it occurs also in Querétaro, which lies between the above two states, and possibly also in the northeastern part of Jalisco. The type locality has been restricted to Zimapán, Hidalgo, Mexico, by Smith & Taylor (1950a).

Locality records: MEXICO. *Guanajuato:* León (Smith & Taylor, 1950b). *Hidalgo:* Zimapán (USNM 11370).

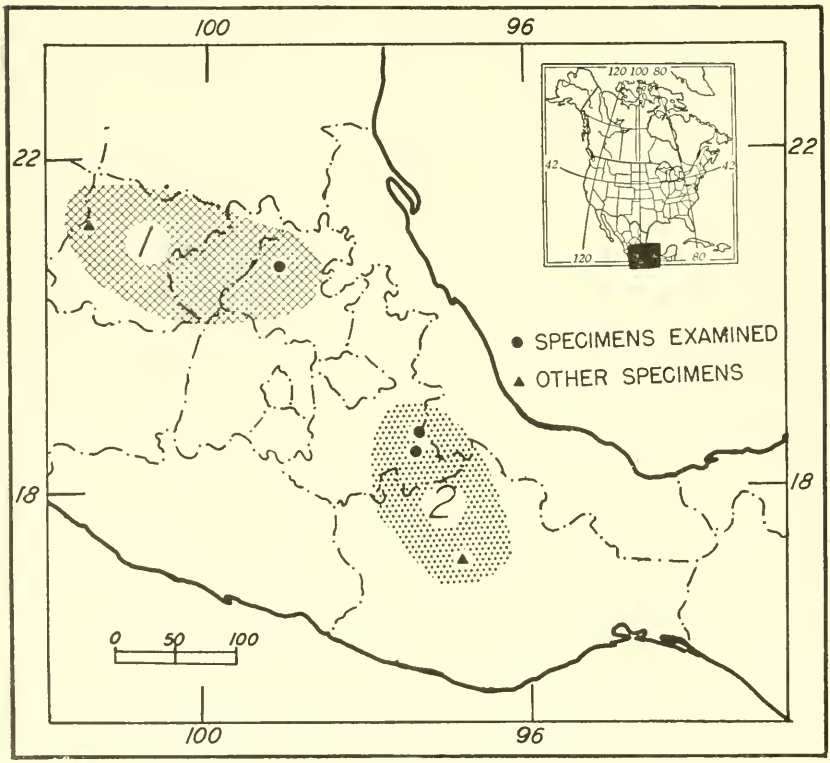

FIG. 12. Map showing the geographic distribution of the species: 1. *Phrynosoma boucardii* and 2. *Phrynosoma braconnieri*.

TABLES

TABLE 1. The number of teeth borne by the premaxillary bone

SPECIES	Number of specimens	Number of teeth
P. cornutum	20 spec.	19 with 4; 1 with 5
P. solare	3 spec.	3 with 6
P. douglassii	4 spec.	4 with 6
P. modestum	1 spec.	1 with 6
P. coronatum	2 spec.	2 with 8
P. orbiculare	1 spec.	1 with 4
P. m'callii	1 spec.	1 with 2

TABLE 2. Actual measurements

		Total length	Snout-vent	Axilla-groin	Arm length	Leg length	Head length	Head width	Eye-snout	Eye-ear	Ear-snout
P. p. goodei											
♂ 8567a	USNM	114	.....	73	38	51	14	14	6	5	14
♂ 8567b	USNM	.....	.....	.....	35	47	.....	snout	crushed		.....
♂ 10166	MVZ	114	.....	70	33	47	14	14	7	4	12
♂ 69653	AMNH	100	.....	63	31	42	14	13	7	4	11
♂ 69654	AMNH	104	.....	64	33	46	14	13	6	5	12
♂ 69655	AMNH	111	.....	67	35	47	15	14	7	5	13
♂ 69656	AMNH	97	.....	60	33	42	13	13	7	5	12
♀ 16693	SSNH....	112	.....	75	36	48	15	15	7	5	13
P. cerroense											
♀ 11977	USNM...	113	84	.....	37	45	16	16	7.5	6.5	14
♀ 24357	LMK ...	114	80	.....	35	46	16	16	8	5	14
♂ 17370	SSNH....	105	70	.....	30	46	16	16	8	5	14
♀ 17369	SSNH....	75	53	.....	26	32	13	12	6	4	11
P. taurus											
♀ 22246	EHT....	62	54	33	29	37	13	13	7	6	12
♂ 23987	EHT....	87	71	49	35	50	16	17	8	7	16
♀ 111368	USNM...	78	66	39	31	42	15	18	8	7	15
♀ 46713	USNM...	75	66	40	37	45	14	17	7	7	14
P. ditmarsi											
♂ 36022	USNM...	105	77	49	42	52	19	23	9	10	20
♀ 36012	USNM...	.....	61	45	35	44	16	19	7	8	17
♀ 557	AMNH..	.....	78	51	41	50	18	22	8	9	20
P. boucardii											
♀ 111370	USNM...	123	79	44	39	51	17	20	9	7	17

From actual measurements made on the specimens studied, I have computed the percentage relationships, according to the following formulae. In the tables the maximum, mean and minimum are recorded. Both male and female are included to show the effect of secondary sexual differences.

FORMULAE

Body	$\frac{\text{snout-vent}}{\text{total length}} \times 100 =$
Head	$\frac{\text{head width}}{\text{head length}} \times 100 =$
Eye-ear	$\frac{\text{eye-snout}}{\text{ear-snout}} \times 100 =$
Frontal	$\frac{\text{frontal width}}{\text{head width}} \times 100 =$
Arm-leg	$\frac{\text{arm length}}{\text{leg length}} \times 100 =$
Arm	$\frac{\text{arm length}}{\text{snout-vent}} \times 100 =$
Leg	$\frac{\text{leg length}}{\text{snout-vent}} \times 100 =$
Tail	$\frac{\text{tail length}}{\text{snout-vent}} \times 100 =$
Eye	$\frac{\text{eye-snout}}{\text{head length}} \times 100 =$

TABLE 3. Percentage measurements

	Body	Head	Eye-ear	Frontal	Arm-leg	Arm	Leg	Tail	Eye
P. p. calidiarum									
Max	♀ 72.4	100.0	63.6	86.8	85.4	55.5	70.0	58.9	53.9
	♂ 66.7	107.0	64.4	88.3	91.0	57.5	76.5	69.1	53.4
Mean	♀ 67.5	95.9	53.3	79.5	77.4	44.0	61.6	52.0	42.7
	♂ 63.5	96.1	55.9	80.8	76.2	50.1	65.9	57.3	47.9
Min	♀ 63.5	87.5	46.1	70.6	68.8	41.8	54.0	42.5	40.0
	♂ 58.1	84.8	46.1	73.4	67.4	44.6	60.3	45.5	41.2
P. p. platyrhinos									
Max	♀ 75.5	109.0	61.5	90.0	83.0	51.0	74.0	52.0	56.0
	♂ 70.0	106.5	60.0	86.7	93.0	57.0	70.0	63.0	53.4
Mean	♀ 68.9	96.9	56.2	79.0	77.2	45.7	59.5	44.4	48.9
	♂ 64.3	97.4	53.5	78.1	76.3	48.3	63.2	55.5	47.9
Min	♀ 65.0	89.0	46 7	70.6	71 5	41.0	52.5	32 6	41.6
	♂ 61.0	87.5	46.7	68.8	67.0	42.0	52.0	40.0	40.0
P. m'callii									
Max	♀ 70.6	100.0	66.6	93.0	84.5	54.2	71.5	65.0	53.9
	♂ 70.1	107.6	66.6	93.3	83.3	58.1	71.0	63.0	52.8
Mean	♀ 66.3	91.4	58.5	83.4	76.1	48.5	62.9	51.0	46.1
	♂ 64.7	90.3	58.7	84.3	75.6	49.7	65.3	55.3	45.9
Min	♀ 60.5	81.4	53.9	66.8	68.0	37.4	55.0	41.7	37.5
	♂ 61.4	85.8	53.3	76.6	68.0	44.2	57.9	50.0	41.2
P. modestum									
Max	♂ 70.8	116.6	66.6	90.0	93.5	58.4	75.0	75.0	60.0
	♀ 72.4	115.1	64.5	91.0	90.5	60.0	70.6	53.4	63.6
Mean	♂ 62.7	103.2	56.0	79.2	79.1	52.2	66.1	57.7	51.5
	♀ 68.8	104.8	57.4	79.1	83.4	50.9	60.9	43.6	54.9
Min	♂ 55.2	92.8	44.4	71.5	72.0	43.5	55.5	47.7	40.1
	♀ 62.9	98.1	45.6	62.3	75.0	45.4	54.0	38.3	48.3

TABLE 4. Percentage measurements

		Body	Head	Eye-ear	Frontal	Arm-leg	Arm	Leg	Tail	Eye
P. c. frontale										
Max.	♀	75.5	112.0	64.0	70.0	87.5	47.4	59.1	46.8	53.0
	♂	72.0	117.5	60.0	72.2	81.4	52.2	67.5	60.0	58.0
Mean.	♀	71.9	103.0	55.0	64.7	78.6	43.1	54.5	39.7	49.7
	♂	67.6	105.7	54.7	67.6	75.5	45.9	61.1	48.1	50.7
Min.	♀	69.5	95.0	50.0	58.0	71.0	39.0	50.0	32.3	45.5
	♂	62.5	89.0	50.0	55.0	70.1	38.2	51.8	38.8	45.0
P. c. blainvillii										
Max.	♀	74.0	117.8	58.0	73.3	85.0	49.5	62.5	48.4	58.0
	♂	68.0	105.5	62.5	75.0	81.0	48.7	67.5	65.0	55.6
Mean.	♀	70.2	104.0	54.1	66.1	77.0	44.1	57.2	43.8	50.3
	♂	63.7	99.2	54.8	68.1	75.1	46.1	61.3	57.3	49.6
Min.	♀	67.5	95.0	50.0	60.0	71.8	40.2	52.0	37.4	45.0
	♂	60.6	91.0	50.0	61.2	68.0	41.8	53.5	46.8	44.5
P. c. schmidti										
Max.	♀	71.2	100.0	60.0	76.5	86.5	49.5	57.5	49.5	56.2
	♂	65.5	100.0	64.2	73.3	78.0	48.5	64.0	59.0	56.2
Mean.	♀	68.6	98.1	56.1	69.6	81.2	43.8	53.9	45.8	51.0
	♂	64.2	96.6	58.5	70.2	74.8	47.1	63.3	58.0	52.1
Min.	♀	66.5	94.1	53.0	61.8	72.5	41.6	50.5	40.3	47.0
	♂	63.5	95.0	55.6	68.5	71.4	45.5	62.5	56.8	50.0
P. c. jamesi										
Max.	♀	70.5	95.0	57.1	86.8	75.5	46.2	60.5	58.5	52.6
	♂	65.0	105.0	57.1	82.5	80.0	51.4	64.4	66.0	50.0
Mean.	♀	68.5	93.4	51.5	73.7	74.0	43.1	57.2	45.6	44.8
	♂	63.5	93.5	54.3	75.5	76.6	47.3	61.7	57.6	46.8
Min.	♀	63.0	88.3	40.0	72.2	72.0	36.5	50.0	41.7	35.3
	♂	60.2	84.0	50.0	63.1	73.0	45.7	60.0	53.5	44.5

TABLE 5. Percentage measurements

	Body	Head	Eye-ear	Frontal	Arm-leg	Arm	Leg	Tail	Eye
P. c. coronatum									
Max	♀ 71.5	104.5	60.0	80.0	83.5	52.4	65.7	52.4	50.0
	♂ 66.5	100.0	62.5	93.4	81.0	50.8	65.0	60.0	52.6
Mean	♀ 68.2	90.8	55.9	71.3	77.7	47.7	61.3	47.4	46.6
	♂ 64.3	91.4	56.1	76.3	75.1	47.4	62.4	55.5	47.9
Min	♀ 65.6	79.0	52.6	54.2	69.0	42.3	57.5	42.5	41.2
	♂ 62.5	79.0	53.4	64.8	66.0	42.7	60.5	50.6	44.4
P. asio									
Max	♀ 66.7	110.0	56.2	83.3	88.4	54.9	70.2	62.0	55.0
	♂ 64.5	100.0	56.2	82.9	80.5	52.9	65.0	74.3	55.0
Mean	♀ 64.0	96.1	51.9	73.4	81.6	49.7	61.3	56.4	49.1
	♂ 55.7	98.0	53.3	78.5	76.9	49.1	62.6	67.7	52.0
Min	♀ 61.7	90.0	43.7	60.0	72.4	43.9	56.6	50.0	41.2
	♂ 41.0	94.5	52.4	71.5	67.7	40.7	60.5	54.9	50.0
P. cornutum									
Max	♀ 76.7	109.6	58.3	87.7	90.0	32.8	32.4	56.2	69.9
	♂ 75.1	112.6	61.7	81.5	88.5	33.2	35.0	55.8	70.0
Mean	♀ 72.8	101.5	49.0	74.1	80.1	27.5	28.5	48.8	60.7
	♂ 68.4	103.6	49.4	73.2	77.7	26.7	28.8	49.8	64.1
Min	♀ 68.5	94.4	42.1	66.7	71.2	23.3	24.3	40.6	52.5
	♂ 59.4	96.0	42.8	66.3	68.9	22.5	25.0	44.6	55.8
P. solare									
Max	♀ 78.9	108.5	64.2	82.7	89.4	53.6	62.4	40.0	47.4
	♂ 68.0	95.2	62.6	80.0	82.5	60.0	62.5	57.4	45.4
Mean	♀ 73.3	98.1	55.7	70.8	83.5	44.3	53.2	36.2	42.1
	♂ 66.4	88.0	56.2	72.5	76.0	46.0	58.4	50.7	41.5
Min	♀ 71.4	87.5	47.4	63.2	77.5	38.2	42.6	26.9	38.8
	♂ 63.5	81.0	53.0	61.2	68.8	38.8	53.2	47.5	39.1

TABLE 6. Percentage measurements

	Body	Head	Eye-ear	Frontal	Arm-leg	Arm	Leg	Tail	Eye
P. d. douglassii									
Max.	♀ 74.5	131.0	60.0	66.6	93.0	52.5	66.0	51.0	58.4
	♂ 67.0	122.0	55.0	66.5	76.0	50.0	66.0	58.0	55.0
Mean	♀ 70.9	118.1	52.7	61.1	81.1	45.2	56.6	41.3	54.7
	♂ 65.2	120.0	52.5	65.1	73.7	45.8	62.2	52.5	54.7
Min.	♀ 66.5	108.0	46.1	53.0	67.5	35.0	47.0	34.0	45.5
	♂ 63.5	118.0	50.0	63.6	71.5	41.7	58.5	47.0	54.5
P. d. ornatum									
Max.	♀ 72.5	130.0	55.6	70.5	81.1	46.7	61.5	46.5	58.0
Mean	♀ 70.7	120.1	43.8	57.8	73.8	41.1	54.8	42.0	49.8
Min.	♀ 69.6	101.2	40.0	52.4	66.7	37.5	50.0	38.0	46.2
P. d. hernandesi									
Max.	♀ 72.0	143.0	52.7	60.7	86.3	47.4	65.7	53.0	58.9
	♂ 67.0	143.0	53.4	58.4	81.6	50.0	65.4	58.4	57.0
Mean	♀ 69.6	126.7	47.5	56.1	76.7	43.9	56.7	44.6	50.4
	♂ 65.1	125.4	50.5	54.6	78.1	48.3	61.2	53.7	52.5
Min.	♀ 65.6	113.8	42.1	47.8	71.8	36.5	47.6	36.9	44.4
	♂ 63.1	111.6	47.0	50.0	74.5	44.8	53.8	49.4	47.0
P. d. ornatissimum									
Max.	♀ 74.2	131.1	50.0	61.1	83.4	47.0	59.5	50.0	56.2
	♂ 70.1	133.2	56.5	64.4	85.7	53.8	64.8	54.8	54.2
Mean	♀ 70.1	123.8	47.5	57.6	76.8	44.7	56.2	43.2	52.5
	♂ 67.2	117.4	52.2	60.7	83.3	50.6	60.7	48.9	51.9
Min.	♀ 66.7	120.2	44.4	52.2	76.6	43.1	53.5	34.6	50.0
	♂ 64.5	106.0	50.0	61.2	77.8	48.0	57.6	42.8	50.0

TABLE 7. Percentage measurements

		Body	Head	Eye-ear	Frontal	Arm-leg	Arm	Leg	Tail	Eye
P. d. brevirostre										
Max.	♀	77.5	141.0	53.4	66.8	87.2	48.4	66.0	46.6	57.1
	♂	67.5	133.0	58.4	66.8	86.0	52.3	64.5	70.4	63.5
Mean	♀	70.9	127.4	50.6	56.6	80.9	43.0	53.3	41.5	53.9
	♂	65.4	119.0	53.2	62.1	80.6	43.0	59.4	54.7	53.6
Min.	♀	68.0	113.0	47.0	52.6	73.0	38.6	49.4	36.8	50.0
	♂	60.1	108.0	46.1	57.1	74.0	40.0	54.0	48.2	46.7
P. o. orbiculare										
Max.	♀	72.0	122.0	53.4	66.6	85.0	49.3	66.2	61.6	55.6
	♂	67.0	112.7	53.4	73.5	81.0	52.8	65.2	77.8	52.6
Mean	♀	66.5	108.9	49.5	56.6	77.2	43.7	56.9	50.7	48.3
	♂	61.4	104.1	52.1	61.7	76.4	47.1	61.6	62.9	48.1
Min.	♀	62.0	100.0	39.0	50.0	67.5	38.2	49.4	39.0	36.8
	♂	56.4	94.1	47.0	55.5	73.0	41.2	56.1	49.2	42.0
P. o. cortezii										
Max.	♀	69.0	119.0	54 0	64.0	87.0	52.0	60.8	55.4	53.0
	♂	62.6	117.5	53.4	62.2	81.5	50.0	63.2	65.2	53.2
Mean	♀	66.3	114.4	50.8	56.6	77.2	43.5	56.6	50.8	49.2
	♂	61.9	112.9	49.7	59.8	78.7	46.3	58.2	61.7	48.4
Min.	♀	62.8	107.0	46.0	52.4	73.2	36.0	49.2	44.8	45.2
	♂	60.5	108.7	47.0	58.0	75.2	41.7	55.0	60.0	44.5

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The Crayfishes of Kansas

BY

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ABSTRACT: Three genera of crayfishes, including seven species, are reported from Kansas. Their taxonomy, distribution and ecology are discussed. A general discussion of the natural history of crayfishes is given. Nearly all distributional data presented are the results of field work done since 1946. Records from the literature have been checked where possible and a statement is included concerning the disposition of J. Arthur Harris' early collection of crayfishes from Kansas.

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INTRODUCTION

PURPOSE OF THE STUDY

This study was undertaken in order to determine the kinds of crayfishes in Kansas and their distribution within the state. However, the scope of the paper has been broadened somewhat in order to make a general knowledge of crayfishes available to interested persons whether or not they have had special training in biological sciences. This general information is neither new nor original, and has been presented in numerous other papers, but we include it here because these papers may not be readily available to the reader.

NATURAL HISTORY [1]

Habitat: Crayfishes are the largest crustaceans inhabiting the fresh waters of central United States. They exist in habitats varying from clear mountain streams to lakes, ponds, swamps, overflow pools along rivers and creeks, to burrows in mud near streams or ponds, or in poorly drained soils. A species is usually restricted to one type of habitat. The kinds of crayfishes that live in holes or burrows in poorly drained soils are commonly found only in such places, and similarly the kinds that live in clear streams are not commonly found elsewhere. A few species of crayfishes are restricted entirely to caves or underground watercourses in certain areas in Alabama, Florida, Indiana, Kentucky, Missouri, and Tennessee.

Molting: Crayfishes along with insects, spiders, ticks, and other invertebrates with jointed legs, belong to a group of animals known as the Arthropoda. All Arthropoda possess an outer covering called an exoskeleton. The exoskeleton is hard in some types of Arthropoda and relatively soft in others, but in all Arthropoda including crayfishes the exoskeleton must be shed or molted periodically in order to allow the animal to grow. As the animal grows inside the more or less rigid exoskeleton, the animal becomes more and more restricted for space in which to expand. The exoskeleton, like a belt which has become too small and lacking extra space or holes for lengthening, must be discarded for a new and larger one. Actually molting is a complex process, but suffice it to say that as the old exoskeleton becomes too small to permit further growth of the crayfish, a new soft exoskeleton is secreted under the old hard exoskeleton. When this new soft exoskeleton is complete and the crayfish is ready to molt, it hides in some protected place, swells itself

1. See glossary for definitions of terms.

with water, bursts open the old exoskeleton and pulls itself completely out of its old body covering. Even the lining of the esophagus, stomach, fore and hind intestine are left behind with the old exoskeleton. Molting is a violent shock to these animals, and many individuals do not survive the process. The freshly exposed new exoskeleton is soft, and for a time after the old exoskeleton is shed the crayfish is completely limp. Gradually the new larger exoskeleton hardens. Contrary to popular belief, crayfishes which have a soft exoskeleton (so called "soft craws") are not a "special" species of crayfish, but are merely crayfishes of any species undergoing a phase of molting.

Reproductive phenomena:[2] In order to understand certain aspects of the life cycle of crayfishes as well as certain details concerning the classification of crayfishes, it is necessary to understand the specialized reproductive structures and mating behavior of these animals.

Male crayfishes possess a specialized pair of appendages known as gonopods, which are modified swimmerets located posterior to the last pair of walking legs. The gonopods serve as sperm guides during copulation. Tubes (vasa deferentia) which conduct sperm from the testis located inside the body, open to the exterior on the medial side of the bases of the last pair of walking legs. The gonopods serve the purpose of aiding in the transportation of sperm from these openings to the annulus ventralis of the female during copulation.

Male crayfishes of the subfamily Cambarinae (those crayfishes occurring east of the Rocky Mountains in the United States) exist in what are termed two "forms" which are designated as form I and form II. Reproductively inactive male crayfishes are form II and are characterized by gonopods which have relatively thick, noncorneous terminal processes. Form I males are in a reproductively active state and are characterized by gonopods which have distinct corneous terminal processes. Either form male can change into the other form by molting.

The gonopods of the form I male are one of the most constant morphological structures exhibited by these crayfishes, and the distinctions between species are based in large part on the number, shape, and arrangement of the processes on these appendages. We follow Hobbs (1940:46) in naming the processes on the gonopods.

2. See E. A. Andrews, 1906. The Annulus Ventralis. Proc. Boston Soc. Nat. Hist., vol. 32, No. 12, pp. 427-479, 2 figs. in text, pl. 43-48, for good summary of breeding process.

For purposes of description the gonopod is considered to be directed ventrad. Thus the side of the gonopod that is dorsal in normal position is termed the cephalic border, and the side that is ventral in normal position is considered the caudal border.

Female crayfishes possess a sperm receptacle known as the annulus ventralis, which is situated on the sternum between the last two pairs of walking legs. The annulus ventralis is not a tube leading into the body of the female crayfish, but is merely a cuplike structure.

The annulus ventralis is a structure which has some importance in classification of crayfishes. Its structure, while not as constant as that of the form I male gonopods, is on the whole a fairly good diagnostic character for species of crayfishes. This is especially true among the crayfishes of Kansas.

Mating: Mating is accomplished in the following manner. The male grasps the female's appendages with his chelate legs, turns her on her back and approaches her in such a manner that the ventral sides of both crayfishes are in close contact. The male maintains a firm grasp on the female's appendages with his chelate legs as well as by means of hooks on his third pair of walking legs, and directs the tips of the gonopods against the annulus ventralis of the female. The female remains passive throughout this process. Mating pairs may remain thus attached for over an hour, and they are so firmly attached that they may be thrown into boiling water without becoming disengaged.

During the mating process the ends of the vasa deferentia, the gonopods and the modified second pair of swimmerets all fit together in such a manner as to form a tube through which the sperm flow into the annulus. The sperm are deposited in a twisted blind tube which lies within the body of the annulus. The depression in the annulus ventralis is plugged with a waxlike deposit at the conclusion of copulation. This plug is apparently a secretion from the male.

Egg laying: Female crayfishes do not normally molt between the time of mating and the hatching of young. Egg laying occurs quite some time after the last preceding molt, consequently the exoskeleton is often covered with algae and other debris. Just prior to egg laying the female begins to clean the ventral side of the abdomen, the swimmerets, the annulus ventralis and surrounding parts. She uses the fifth walking legs as a brush to scrape or sweep away the debris, or sometimes uses the chelate walking legs

to pick off firmly attached objects. Part of the cleaning process is accomplished while the female lies on her back. During this time the female is extremely nervous, and if she is excited two or three times in succession she may die.

When the abdomen has been cleaned and the female is ready to lay eggs she first finds a secluded place, then stands well off the ground on her legs and allows a secretion from "cement glands" on the ventral side of the abdomen to run down over the swimmerets. This secretion swells up to form a transparent mucoid mass which hangs down from the swimmerets. This accomplished, the female folds the abdomen under the thorax, rolls over on her back and spreads out the tail fan, thus spreading the secretion over the bases of her walking legs as well as the ventral surface of the thorax. A sort of mucous filled cup or trough is formed by the tail fan and the pleurae of the abdominal segments. While still in this position the outlets of the oviducts are opened, the eggs are passed out of the oviducts, over the troughlike sternal plate anterior to the annulus, then over the annulus and finally into the trough formed by the flexed abdomen. Presumably the sperm fertilize the eggs as they pass across the annulus ventralis, and there is evidence that the female by the use of surrounding parts is actually able to force sperm from the annulus ventralis when the eggs are being laid. On the other hand the sperm may be swept through the mucoid mass from the "cement glands" into the oviducts before the eggs are laid thus making fertilization internal. No one knows exactly how the eggs of crayfishes are fertilized.

Finally the eggs become fastened to the swimmerets. The females carry these eggs for various lengths of time. Such females are said to be "in berry." Presumably the mucous secretion of the "cement glands" of the abdomen fastens the eggs to the swimmerets, but the actual mechanism of attachment is unknown.

Life history: Little is known concerning the life histories of crayfishes; only a few species have been studied intensively, and none has been studied in the region west of the Mississippi river.

The life history of *Orconectes immunis,* one of the species of crayfishes occurring in Kansas, has been studied by Tack (1941: 425) in ponds at the Cornell University Experimental Fish Hatchery at Ithaca [Tompkins Co.], New York. Tack found that the mating season of *O. immunis* extended over a period of several months, beginning as early as June 16, and continuing as late as October 12. Mating frequency reached its peak in late August, after which it declined rapidly. From these studies, it appears that this species

of crayfish mates in the summer and early fall. Males or females may mate with more than one individual.

Orconectes immunis females at Cornell lay eggs chiefly in the months of October and November. Females carry the eggs through the winter and the eggs hatch about mid May. Newly hatched young are called first stage young. They are attached at the telsons by means of a slender thread to the old egg shells (and thence to the swimmerets of the mother). The young have chelae which are hooked at the tip and they soon grasp this slender thread with these hooked chelae and remain attached mainly by the chelae. This double means of attachment prevents the young from being lost from the mother. After a few days (about a week) the juveniles molt into the second stage young which are still attached by the telson threads and which have hooked chelae that grasp the attachment thread. In about a week these individuals molt into the third stage young which are not permanently attached to the mother and do not have hooked chelae. A few days later these crayfishes molt into the fourth stage. The annulus ventralis of the young females shows some differentiation and small buds which will be the gonopods appear on the young males. The fourth stage is followed in approximately a week by the fifth stage by which time the configuration of the adult annulus ventralis is beginning to appear in the females and the gonopods of the males are definitely formed. This and a few successive stages are collectively spoken of as the juvenile stages and they persist throughout the first summer of the crayfish's life. Molting ceases at the end of the first summer with the onset of cold weather. By this time a few of the year's crop of young have become mature, but most of them do not mature until later.

A general spring molting for all individuals except those females which are bearing eggs, occurs at the onset of spring with the increasing activities of the crayfishes. Large males which were form I (mature) during the preceding fall and winter molt into the form II (sexually inactive state), while males that pass the winter in the form II state remain form II. Depending on the size of the individual the crayfishes molt once or twice during their second summer, the larger individuals molting only once. Most of the males molt into form I at this time, and these are the males which mate in the fall breeding season.

A majority of the form I breeding males die at the conclusion of the breeding season in the fall, but a few of these individuals survive the winter and die in the spring. The majority of adult

females die in the spring during and succeeding the spring molt after the eggs have hatched.

Economy: The crayfish's value as fish bait is well known to fishermen. In certain regions of the country, especially the south, crayfishes are esteemed as human food, but perhaps their greatest use as food is by such animals as bass, catfish, raccoon, heron, and other predators. Observations made by Williams and the observations of others have shown that crayfishes will eat almost any kind of organic material. They have thus a useful position as convertors of organic materials into food for such animals as certain fishes, turtles, raccoons or men.

Especially in portions of the southern states burrowing species of crayfishes have proved troublesome to agricultural interests by burrowing holes in dikes and pond dams, and by foraging on young cotton and corn plants at night.

METHODS OF CAPTURE

Traditional practices of catching crayfishes on fishing lines or with bacon tied to the end of a string are hardly adequate when a large series of specimens is desired. A geographic distributional study such as this one requires large series of specimens including males, females and juveniles from all major drainage systems within the area concerned. For the species which live in ponds or streams we have found seining with a minnow seine to be the most effective method of collecting. A seined area should be worked several times in succession because agitation of the water apparently causes many crayfishes to come out of hiding into the open water. In rocky streams where seining is difficult a fine mesh cloth dip net has been used. Crayfishes like dark places. We have found that a dip net dyed black is an aid to capture. A crayfish seen on the bottom of a gravelly stream can be induced to swim into a black dip net either with the hand or better with a dark colored stick. Crayfishes are apparently accustomed to seeing sticks in the water, and can actually be pushed into a net with little or no resistance on their part if such a stick is used; or one can pin them to the bottom of a stream or pond with a forked stick. Many times, specimens can be secured by turning over rocks, tin cans, logs, boards, weeds or any debris found in the water. Burrowing species can sometimes be captured at the mouths of their burrows, especially in the spring of the year. Usually the burrowing types have to be dug out.

Methods of Preservation

Our practice has been to drop specimens into five percent formalin in glass jars in the field. Specimens are thoroughly washed in running water for several hours when returned to the laboratory and are then transferred to seventy percent alcohol.[3]

Historical

Previous distributional and species records in Kansas were based on collections from scattered localities over the state or were based on the collections made by J. Arthur Harris, principally in the counties bordering the Kansas river in the northeastern portion of Kansas.

James Arthur Harris, 1880-1930, did his undergraduate and master's degree work at Kansas University between 1898 and 1902. His major interest was botany, but that he had an active interest in zoology is exemplified by his papers on Kansas crayfishes.

When the present study was begun at least a portion of Harris' collection was still housed at the University of Kansas, but the collection had seriously deteriorated. Many specimens were dried and broken, some were poorly preserved, and locality data had been lost or was incomplete. Consequently most of the collection was considered worthless and was discarded.

The first mention in the literature of a crayfish from Kansas is Faxon's report (1885a:113) of *Cambarus simulans* from Fort Hays [Ellis Co., Kans.]. Faxon (1885b:71, 96, 99) listed new locality records in Kansas; and later (1885d:140-142) he published a preliminary catalogue of the crayfishes of the State in which he listed seven species and one variety, including in this paper descriptions of two new species, *Cambarus nais,* Labette Co., Kansas, and *Cambarus neglectus,* Mill Creek, Wabaunsee Co., Kansas. Faxon (1890:621, 622, 630, 632) later listed new locality records for the state. W. P. Hay (1900:121-122) described *Cambarus pilosus,* Beloit, Mitchell Co., Kansas. J. Arthur Harris (1900:263-274) published the first of his papers dealing with the Kansas crayfishes, which was followed by an abstract of this paper (1901:115). He subsequently published a distributional study of Kansas crayfishes (1902:1-11) and later (1903:51-187) his ecological catalogue of crayfishes belonging to the genus *Cambarus.* From that date until the present little work dealing specifically with the crayfishes of

3. We will welcome an opportunity to study specimens collected from any part of the state, especially the areas which are not thoroughly covered in this study. Specimens with full locality data included, should be placed in jars of preservative, packed in a tight container and mailed to us. Specimens can be left in five percent formalin indefinitely.

Kansas has been done. Creaser and Ortenburger (1933:42) reported the occurrence of *Cambarus blandingii acutus* in Kansas (which extensive collecting has failed to verify), and later Creaser (1933:7) described *Faxonius luteus* which he reported as occurring in Kansas. Finally, Creaser (1933:15) added a new locality record for *Faxonius immunis pedianus*.

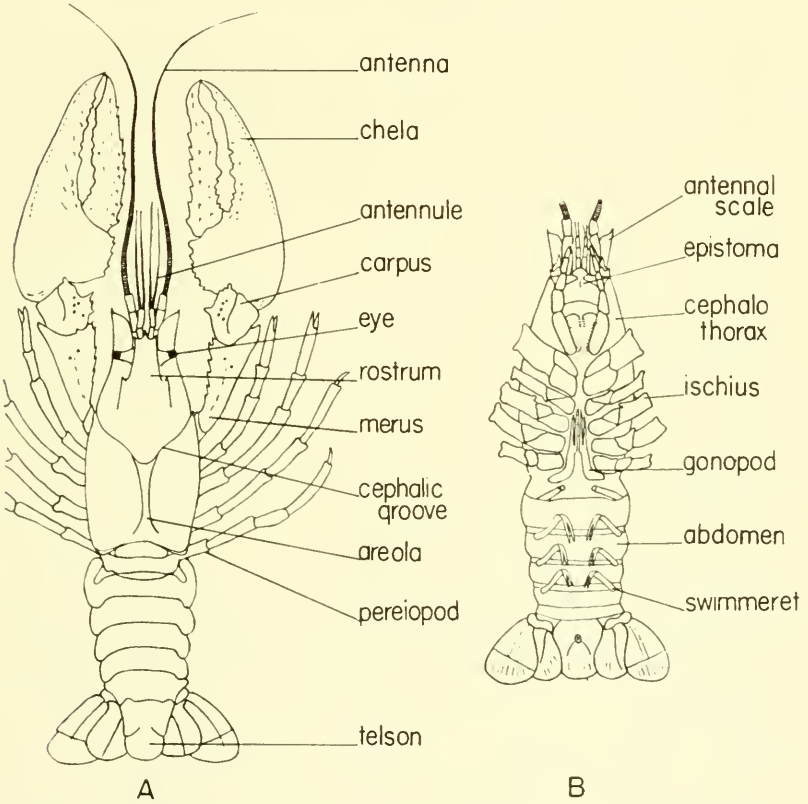

FIG. 1. Generalized figure of crayfish showing some important structures. A. Dorsal view. B. Ventral view with parts of appendages removed.

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GLOSSARY OF COMMON TERMS USED IN IDENTIFICATION OF CRAYFISHES

Acumen: tip of rostrum.

Adventitious process: process on caudolateral or lateral border of *Procambarus* gonopods, corneous, thin and bladelike in form I males.

Appendages: any of the "feelers", legs, or other jointed projections from the body.

Annulus ventralis: sperm receptacle on sternum of female between posterior two pairs of walking legs.

Anteapical: just behind the apex or tip.

Antenna: long whiplike "feeler".

Antennal scale: lateral bladelike structure at base of antenna.

Anterior: front, nearest the head end.

Apical: apex or tip.

Areola: usually hourglass-shaped area lying dorsally over mid-sagittal plane of thorax; bounded by grooves or lines which delimit dorsomedial limits of gill chambers.

Bispinous: with two spines.

Branchiostegite: lateral side of thorax covering gill chamber.

Carina: median dorsal spindle-shaped eminence near tip of rostrum.

Carpus: fifth joint distad on legs.

Caudad (caudally): toward the back or tail end.

Caudal process: minute terminal process on caudal border of *Procambarus* gonopod; corneous in form I males.

Central projection: strong projection formed by fusion of so called centrocephalic and centrocaudal processes; located centrally on tip of *Procambarus* gonopod, laterally on *Orconectes* and *Cambarus* gonopod; corneous in form I male.

Cephalic: pertaining to the head.

Cephalic groove: sinous, oblique groove separating cephalothorax into an anterior and posterior portion.

Cephalic process: process located cephalomedially on tip of *Procambarus* gonopod.

Chela (chelate): pincer or claw; large chelae sometimes called the hands.

Corneous (cornified): horny texture.

Crustaceans: Arthropods which breathe by means of gills, have a chitinous exoskeleton impregnated with calcium salts.

Distal: away from the mid-line of the body; toward the tips of the appendages.

Dorsal: toward the back side or top side of the animal.

Epistoma: plate on ventral side of head which bears a roughly triangular shaped cephalic extension.

Gonopod: modified first abdominal swimmeret of male.

Head: portion of cephalothorax anterior to cephalic groove.
Ischius: third joint distad on legs.
Lateral: to the side.
Lateral rostral spines: spines lateral to acumen on cephalic border of rostrum.
Medial: toward the middle.
Medial process: process located caudomedially on *Procambarus* gonopod; medially on *Orconectes* and *Cambarus* gonopod.
Median: in the middle; the mid-line.
Meros: fourth joint distad on legs.
Mid sagittal plane: in the mid-line; a dorso ventral plane in the mid-line running antero posteriorly.
Morphological: pertaining to form or structure.
Mucous (mucoid): thick gummy secretion.
Obsolescent: underdeveloped, nearly absent.
Pereiopod: any of the walking or large chelate legs.
Pleurae: overhanging plates on sides of abdominal segments.
Postorbital ridge: ridge on dorsolateral aspect of head, caudolateral to and nearly continuous with sides of rostrum.
Posterior: toward the back or tail end.
Predator: organism which captures and eats animals.
Process: any of variously shaped "points" or "teeth" at distal end of gonopods.
Proximal: toward the body; especially of an appendage; that portion of a leg which is nearest the body.
Punctations: Little pits.
Rostrum: dorsomedian cephalic extension of head partially covering eye stalks and bases of antennae and antennules.
Sinuous: wavy or serpentine in shape; undulating.
Sinus: a cavity.
Species: (working definition) a group of organisms which interbreed freely in nature.
Spine: any sharp pointed eminence not on gonopods.
Squamous: flat, scalelike.
Sternum: ventral more or less flat plate situated between the walking legs.
Suborbital angle: angulate process on anterior border of cephalothorax below eye.
Telson: terminal, median caudal "fin".
Terminal: pertaining to the end or tip.
Thorax: portion of cephalothorax posterior to cephalic groove.
Truncate: giving the appearance of being cut off square on the end.
Tubercle: a low rounded eminence.
Ventral: the underside.

CHECK LIST OF CRAYFISHES OCCURRING IN KANSAS

Family Astacidae
  Subfamily Cambarinae
    Genus *Procambarus* Ortmann 1905
      Section *barbatus* Hobbs 1942
        Group *barbatus* Hobbs 1942
          Procambarus simulans (Faxon) 1885
          Procambarus gracilis (Bundy) 1876

Genus *Orconectes* Cope (1872)
Section *propinquus* Ortmann 1905
Group *rusticus* Ortmann 1905
Orconectes neglectus (Faxon) 1885
Orconectes luteus (Creaser) 1933
Section *virilis* Ortmann 1931
Group *virilis* Ortmann 1931
Orconectes nais (Faxon) 1885
Orconectes immunis (Hagen) 1870
Genus *Cambarus* Erichson 1846
Section *diogenes* Ortmann 1905
Cambarus diogenes diogenes Girard 1852

ARTIFICIAL KEY TO THE CRAYFISHES OF KANSAS

(Based on form I males only)

1. Gonopods ending always in two elongate processes, Genus *Orconectes*, 4
Gonopods never ending in two elongate processes 2
2. Gonopods nearly straight, truncate, terminating in five bladelike or spinous processes . . . . . Genus *Procambarus*, 3
Gonopods stout, terminal processes strongly curved caudad making nearly 90° angle with axis of shaft, *Cambarus diogenes diogenes*
3. Areola obliterated, at least in middle . . . . . *Procambarus gracilis*
Areola not obliterated . . . . . *Procambarus simulans*
4. Processes of gonopods nearly straight, sometimes the lateral process slightly curved caudad, but never both processes curved in same direction 5
Processes of gonopods both curved caudad 6
5. Medial side of carpus on great chelate legs with long cephalic spine and shorter blunt caudal spine . . . . . *Orconectes neglectus*
Medial side of carpus on great chelate leg with cephalic spine only . . . . . *Orconectes luteus*
6. Tips of processes of gonopods slightly curved caudad making considerably less than 90° angle with axis of shaft, *Orconestes nais*
Tips of processes of gonopods greatly recurved making nearly 90° angle with axis of shaft . . . . . *Orconectes immunis*

ARTIFICIAL KEY TO THE CRAYFISHES OF KANSAS

(Based on females only)

1. Annulus vertralis freely movable, not firmly fused to sternum, Genus *Procambarus*, 2
Annulus ventralis not freely movable, firmly fused to sternum . . . 3
2. Areola obliterated, at least in middle . . . . . *Procambarus gracilis*
Areola not obliterated . . . . . *Procambarus simulans*
3. Rostrum greatly curved downward . . . *Cambarus diogenes diogenes*
Rostrum never greatly curved downward . . . Genus *Orconectes*, 4
4. Areola at narrowest point wider than postorbital ridge 5
Areola at narrowest point not wider than postorbital ridge . . . 6

5. Medial side of carpus on great chelate legs with long cephalic spine and shorter blunt caudal spine . . . . . *Orconectes neglectus*
   Medial side of carpus on great chelate leg with one spine only, *Orconectes luteus*
6. Antennal scale truncated at anterior margin . . . . *Orconectes immunis*
   Antennal scale not truncated at anterior margin . . . *Orconectes nais*

Procambarus simulans (Faxon)

Plate XCI and Text Fig. 2

Cambarus simulans Faxon, 1885, Proc. Amer. Acad. Arts and Sci., vol. 20, no. 7, pp. 112-113.
Cambarus gallinus Cockerell and Porter, 1900, Proc. Acad. Nat. Sci. Philadelphia, p. 434.
Cambarus baumgartneri Harris [*nomen nudum*], 1901, Trans. Kansas Acad. Sci., vol. 17, p. 115.
Procambarus simulans Hobbs, 1942, Amer. Midl. Nat., vol. 28, no. 2, p. 342.

Recognition Characters

Male form I: (Plate XCI, fig. F) Rostrum broad at base with convex sides converging abruptly near apex to short acumen, broadly excavated, acumen terminating short of antennal scale; each postorbital ridge ending in low anterior spine, lateral to but nearly continuous with lateral edges of rostrum; suborbital angle obtuse; cephalothorax ovate, punctate dorsally, granulate laterally; cephalic groove continuous laterally; lateral spine sharp, poorly developed; sides of areola not parallel, narrowest width allowing 2-3 rows of punctations; head length contained in cephalothorax length 1.43-1.61 times; telson subtruncate with from 2-5 caudolateral spines, most lateral spine largest; antennae shorter than body; antennal scale (Plate XCI, fig. G) unevenly rounded medially, widest posterior to midlength, subtruncate anteriorly, weak apical spine; chelae elongate, fingers long, not agape; palm squamously tuberculate dorsally, medially, and laterally, tubercles more numerous laterally and medially forming single irregular row along medial border of palm; ventral aspect of hand punctate, with or without scattered tubercles; fingers tuberculate proximally, punctate distally; distal cutting edges of fingers smooth, sharp; immovable finger with prominent rounded proximal tubercle and smaller distal tubercle on ventral aspect of cutting edge; movable finger with two prominent tubercles proximally; carpus with single prominent medial spine continuous with row of ventral spines; scattered tubercles ventrally; dorsal aspect of meros with two short anteapical spines continuous with row of obsolescent spines, ventral biserial row of sharp spines; anterior process of epistoma broader

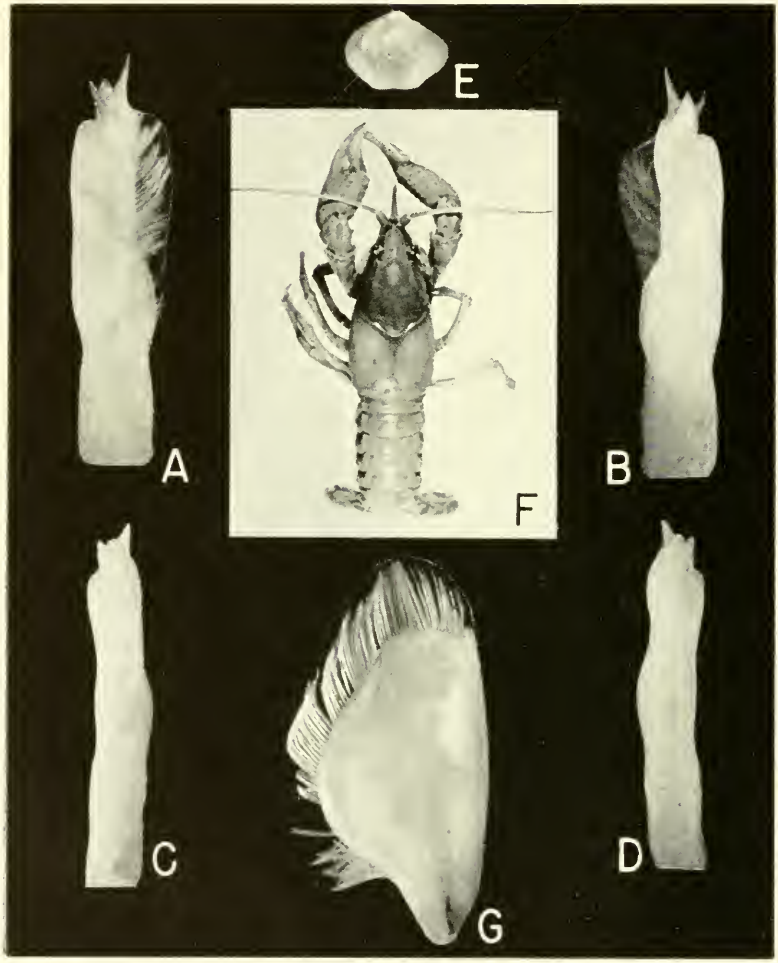

PLATE XCI

Procambarus simulans (Faxon)

FIG. A, ♂ form I gonopod, medial view, × 5.
FIG. B, ♂ form I gonopod, lateral view, × 5.
FIG. C, ♂ form II gonopod, medial view, × 5.
FIG. D, ♂ form II gonopod, lateral view, × 5.
FIG. E, Annulus ventralis, × 5.
FIG. F, ♂ form I, × ½.
FIG. G, Antennal scale, × 5.

than long, lateral sides convex, acute anterior median spine; ischius of third pereiopods with strong hook.

Gonopods (Plate XCI, figs. A, B.) straight, truncate, terminating in six processes: a long curved noncorneous medial process; a shorter noncorneous cephalic process; a corneous centrocephalic process and a corneous centrocaudal process fused to form a long curved central project; and a small thick partially cornified bladelike caudal process medial to a large lateral cornified bladelike adventitious process.

Male form II: Chelae shorter and less powerful than in male form I; terminal processes of gonopods (Plate XCI, figs. C, D.) not cornified.

Female: Chelae shorter and less powerful than male form I; sinus in annulus ventralis (Plate XCI, fig. E.) with no overhanging borders; anterior margin of annulus more or less toothed; annulus divided by a sinuous sinus originating to left of mid-sagittal plane on anterior border, extending obliquely caudad to right, then curving broadly caudad to left of mid-sagittal plane terminating caudally in mid-sagittal plane.

Variations: The annulus ventralis shows individual variations ranging from an extremely toothed anterior border to a condition in which the anterior border is nearly smooth. An aberrant form I male in Lot 267 from McPherson County has an imperfectly developed hook on the ischius of the right second pereiopod.

Ecological Notes

Harris (1902:4) reported *P. simulans* from burrows in a slough that was near a spring-fed pool. The burrows were two inches in diameter, perpendicularly 3 feet deep, and ended in a chamber 10 inches in diameter on a hard pan of shale. The burrows had chimneys at the surface, and he reported that three or four burrows entered one of the underground chambers. Female specimens collected 4 mi. NE Caldwell, Sumner County, Kansas in August, 1901, were carrying eggs. Harris (1903:128) reported a personal communication as saying that *P. simulans* burrowed in the banks of lakes and rivers where they live in New Mexico. They were observed especially in quiet pools in the Gallinas River [New Mexico] which is a swiftly flowing mountain stream with a rocky bottom. Females in May bore eggs. Harris in the same paper (p. 129) recorded occurrence of the species in an irrigation canal at Roswell, [Chaves County], New Mexico. Many burrows were

found in the sides of the canal, but no chimneys were found at this locality.

Creaser and Ortenburger (1933:43) stated that *P. simulans* is found in muddy streams and ponds and in burrows in the hot part of summer when ponds dry up. Females bearing eggs were found in early September.

Nearly all of the specimens of *P. simulans* that we have collected have been taken in spring and early summer from farm ponds, pools, ditches or from burrows in the banks of these bodies of water, or from burrows in low wet ground. This species is apparently not common in Kansas streams. Individuals have been col-

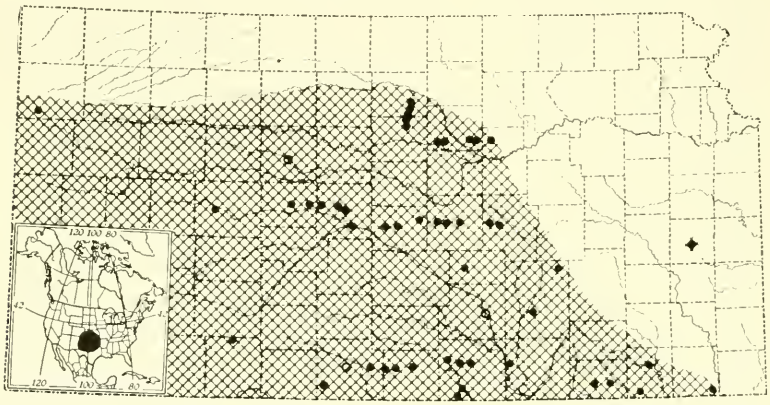

FIG. 2. *Procambarus simulans*, records in Kansas. Inset shows distribution in North America. Open circles = records from literature.

lected from small ephemeral pools in the western part of the State. These pools undoubtedly go dry in the summer of most years. A large collection of *P. simulans* was taken from a muddy pool on 26 March, 1948, Harper County, that had marks of a wheat drill running straight through the edges of the pool. The pool was approximately 10 yards in diameter and had a maximum depth of approximately 1 foot. The pool was located near the top of a hill and was presumable dry in the fall when the wheat was drilled. Presumably this and similar pools were not near permanent water.

Burrow chimneys up to 8 inches in height, composed of mud balls up to one-half inch in diameter are not uncommon. We have observed burrows of *P. simulans* in sandy soil in Barton County, which were 5 inches in diameter either with or without a chimney, in the form of a low crater or completely capped with dried mud. These burrows were more than 2½ feet deep.

Females with young attached have been found in late April.

Records in Kansas

Anderson County: Lot 747. Welda; *Barber County:* Trib. Medicine River: Lot 315. Sharon (sec. 21, T. 32 S, R. 10 W); Lot 316. 1 mi. S Aetna (sec. 21, T. 34 S, R. 15 W); *Barton County:* Lot 202. 3 mi. E Great Bend (SE ¼, sec. 30, T. 19 S, R. 12 W); Lot 203. Cheyenne Bottoms, 2 mi. S Hoisington (NW ¼, sec. 21, T. 18 S, R. 13 W); Lot 204. 1 mi. N, 3 mi. W Hoisington (NW ¼, NW¼, sec. 35, T. 17 S, R. 14 W); Lot 205. 1 mi. N, 3¾ mi. W Olmitz (SW ¼, sec. 29, T. 17 S, R. 15 W); *Butler County:* Lot 297. 14 mi. N, 11½ mi. E Eldorado (sec. 22, T. 23 S, R. 7 E); Lot 300. 2 mi. S Augusta (sec. 3, T. 28 S, R. 7 E); *Chautauqua County:* Lot 128. Davis Creek, 1½ mi. WNW Niotaze, SE¼, sec. 24, T. 34 S, R. 12 E); Lot 730. Roadside ditch, 2⁹⁄₁₀ mi. E Wauneta (sec. 8, T. 34 S, R. 10 E); *Cowley County:* Lot 303. 6 mi. W Winfield (sec. 20, T. 32 S, R. 3 E); *Dickinson County:* Lot 237. 7 mi. N, 6 mi. W Abilene (NE ¼, sec. 7, T. 12 S, R. 1 E); [*Ellis County*]: Lot 737. Hays; *Harper County:* Lot 311. 3 mi. S, 3 mi. W Harper (sec. 28, T. 32 S, R. 7 W); Lot 313. Middle Branch Bluff Creek, 3¼ mi. E Attica (sec. 23, T. 32 S, R. 8 W); Lot 314. West Sandy Creek, 7 mi. W Attica (sec. 19, T. 32 S, R. 9 W); *Harvey County:* Lot 53. [Slough near] Halstead; *Labette County:* Lot 119. 2 mi. W Chetopa (NE ¼, sec. 31, T. 35 S, R. 21 E); *Lincoln County:* Lot 227. Rattlesnake Creek, 10½ mi. N Lincoln (NE ¼, sec. 12, T. 10 S, R. 8 W); Lot 229. 9 mi. N Lincoln (NW ¼, sec. 19, T. 10 S, R. 7 W); *Marion County:* Lot 192. 2 mi. W, 1 mi. N Hillsboro (NE ¼, sec. 31, T. 19 S, R. 2 E); Lot 194. ½ mi. W Lehigh (NW ¼, NW ¼, sec. 27, T. 19 S, R. 1 E); *McPherson County:* Lot 195. 1½ mi. W Galva (SW ¼, sec. 20, T. 19 S, R. 2 W); Lot 196. 3½ mi. W McPherson (SW ¼, sec. 26, T. 19 S, R. 4 W); Lot 197. ¼ mi. W Conway (NW ¼, sec. 26, T. 19 S, R. 4 W); Lot 267. W McPherson City limits (NW ¼, SW ¼, sec. 29, T. 19 S, R. 3 W); Lot 268. 2½ mi. S McPherson (SE ¼, SE ¼, sec. 4, T. 20 S, R. 3 W); *Mitchell County:* Lot 224. 7¹⁄₁₀ mi. S Beloit (NE ¼, NE ¼, sec. 2, T. 8 S, R. 7 W); Lot 225. Fifth Creek, 10½ mi. W Beloit (W ½, sec. 33, T. 8 S, R. 7 W); Lot 226. 16 mi. S, 1 mi. W Beloit (NW ¼, sec. 31, T. 9 S, R. 7 W); *Montgomery County:* Lot 124. 5 mi. E Caney (NW ¼, sec. 11, T. 35 S, R. 14 E); *Ness County:* Lot 209. 4²⁄₁₀ mi. W Ness City SE ¼, sec. 29, T. 18 S, R. 24 W); *Ottawa County:* Lot 232. 1 mi. S, 10½ mi. W Bennington (NW ¼, sec. 17, T. 12 S, R. 4 W); Lot 233. 1 mi. S, 8½ mi. W Bennington (SW ¼, sec. 10, T. 12 S, R. 4 W); Lot 235. E branch of Coal Creek, 6¼ mi. E Bennington (N ½,

sec. 7, T. 12 S, R. 1 W); Lot 236. ¼ mi. N, 9 mi. E Bennington (SW ¼, sec. 4, T. 12 S, R. 1 W); *Rice County:* Lot 198. 13 mi. E, 2 mi. N Lyons (NE ¼, sec. 26, T. 19 S, R. 6 W); Lot 200. ½ mi. W Lyons (SE ¼, sec. 32, T. 19 S, R. 8 W); Lot 201. 5½ mi. W Lyons (NE ¼, sec. 4, T. 20 S, R. 9 W); *Rush County:* Lot 206. 2¾ mi. W Otis (SW ¼, sec. 29, T. 17 S, R. 16 W); Lot 207. ¼ mi. E La Crosse (NE ¼, sec. 34, T. 17 S, R. 18 W); *Sedgwick County:* Stream near Wichita; *Sherman County:* Lot 210. N Smoky Hill River, 10 mi. S, 1 mi. W Goodland (sec. 13, T. 10 S, R. 40 W); *Sumner County:* Lot 50. Chikaskia River, 6 mi. NE Caldwell; Lot 51. Slough 4 mi. NE Caldwell; Lot 304. 3⅒ mi. W Oxford (sec. 17 T. 32 S, R. 2 E); Lot 305. 6 mi. W Wellington (sec. 22, T. 32 S, R. 2 W); Lot 307. West Prairie Creek, 1⅒ mi W, 1½ mi. S Mayfield (sec. 19, T. 32 S, R. 2 W); Lot 309. Chikaskia River, ¼ mi N, ½ mi W Argonia (sec. 7, T. 32 S, R. 4 W).

KNOWN RANGE

Arkansas, Colorado, Kansas, New Mexico, Oklahoma and Texas.

REMARKS

Procambarus simulans has much the same ecological requirements as *P. gracilis.* These two species overlap slightly in their ranges, *P. simulans* having the widest distribution within Kansas, occupying the central, western and southern portions of the State while *P. gracilis* is confined approximately to the eastern one-fourth of the State.

Procambarus gracilis (Bundy)

Plate XCII and Text fig. 3

Cambarus gracilis Bundy, 1876, Bull. Illinois State Lab. Nat. Hist., p. 5.
Procambarus gracilis Hobbs, 1942, Amer. Midl. Nat., vol. 28, no. 2, p. 342.

RECOGNITION CHARACTERS

Male form I: (Plate XCII, fig. F) Rostrum depressed, deeply excavated dorsally, with sides nearly parallel converging gradually to point near apex where sides converge sharply to form small acumen; postorbital ridges distinct, not terminating in anterior spine or tubercle; suborbital angle acute; cephalothorax subcylindrical, laterally compressed, punctate dorsally, head slightly tuberculate laterally, branchiostegite granulate laterally; cephalic groove interrupted laterally; areola narrow, obliterated at middle; head length contained in cephalothorax length approximately 1.72 times; telson evenly rounded, bispinous laterally; antennae shorter than body;

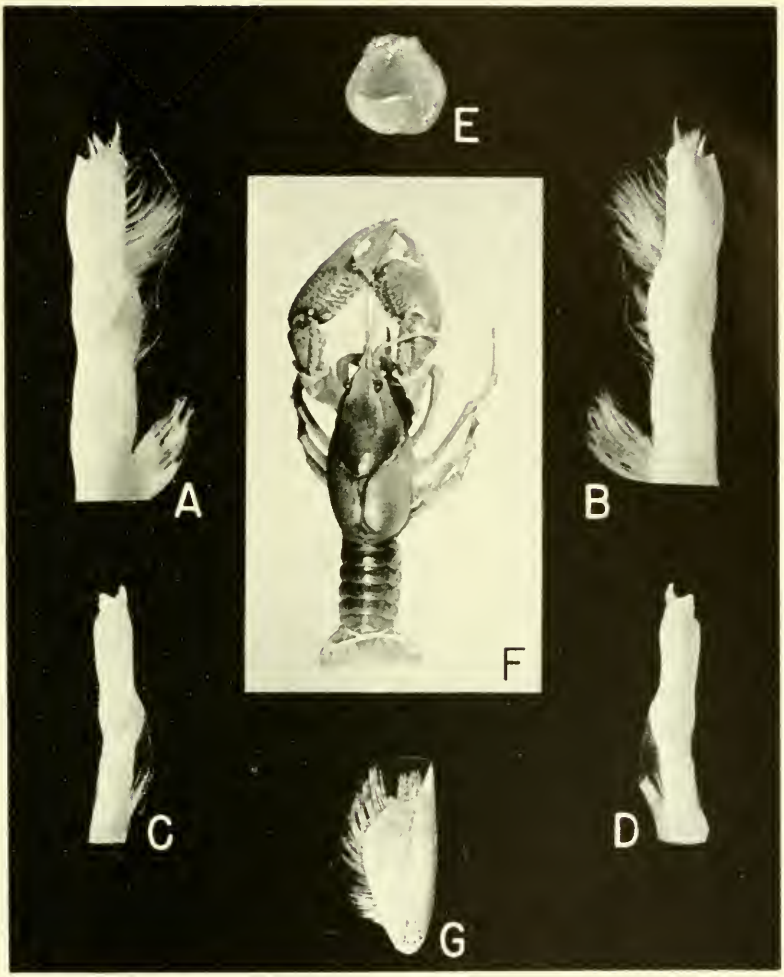

PLATE XCII

Procambarus gracilis (Bundy)

FIG. A, ♂ form I gonopod, medial view, × 5.
FIG. B, ♂ form I gonopod, lateral view, × 5.
FIG. C, ♂ form II gonopod, medial view, × 5.
FIG. D, ♂ form II gonopod, lateral view, × 5.
FIG. E, Annulus ventralis, × 5.
FIG. F, ♂ form I, × ½.
FIG. G, Antennal scale, × 5.

antennal scale (Plate XCII, fig. G) evenly rounded medially, widest anterior to mid-length, terminating in moderately developed lateral spine; chelae narrow, palm heavily muscled, fingers agape; palm and fingers punctate dorsally, laterally and ventrally, with distinct medial row of raised tubercles on palm and proximal half of movable finger; one or two obsolescent rows of tubercles on dorsomedian aspect of palm; opposed edges of fingers each with single row of tubercles of increasing obsolescence distally except for a single raised tubercle near base of each finger and weakly developed distal tubercle on immovable finger; carpus with single median row of spinous tubercles terminating in strong anterior spine; ventromedial aspect of anterior border with curved row of spines terminating in a strong ventral spine; meros with dorsal row of obsolescent tubercles terminating in one to four low anteapical spines; biserial row of spines ventrally; epistoma triangular with sides curved outward; ischius of third pereiopods with hooks.

Gonopods straight (Plate XCII, fig. A, B), terminating in six points which consist of: A noncorneous long curved medial process; a shorter noncorneous cephalic process; a corneous centrocephalic process and a corneous centrocaudal process fused to form a long curved central projection; an extremely small corneous caudal process with accessory lateral point; an adventitious caudolateral corneous bladelike process bent in a right angle with lateral side in line with sagittal plane of body; a small caudal process within right angle formed by adventitious process.

Male form II: Chelae shorter and less powerful than in male form I; tips of gonopods (Plate XCII, fig. C, D) not cornified.

Female: Chelae smaller than in male form I. Annulus ventralis bisected by sinuous sinus with deepest portion to right of midline in anterior half; sinus originating anteriorly at right of midsagittal plane, curving caudad to right, bending sharply to left to cross transverse to body axis, then curving caudad to left, then caudad to right to end in midsagittal plane at posterior border of annulus; anterior portion of annulus (Plate XCII, fig. E) with deep cleft bordered by raised tuberculate margins.

Variations: The degree of excavation of the annulus ventralis shows individual variation, but apparently variation is not consistent in any one locality. Some *P. gracilis* females have annuli which are remarkably similar to the annuli of *P. simulans* females.

Ecological Notes

Bundy (1882:182) reported *Procambarus gracilis* to be very common along water courses in early spring near Normal [McLean County, Illinois], he stated that *P. gracilis* was abundant on prairies near Racine [Racine County, Wisconsin], where it burrowed in low ground emerging at night and after rains. Faxon (1885:58) noted that male *P. gracilis* were rarely found, as did Harris (1903:101). Harris' (1900:265) observations reveal that this species was abundant in stagnant ponds in early spring. Males and females were collected from mouths of burrows in August. Individuals were never taken in creeks. Females were found in early spring with

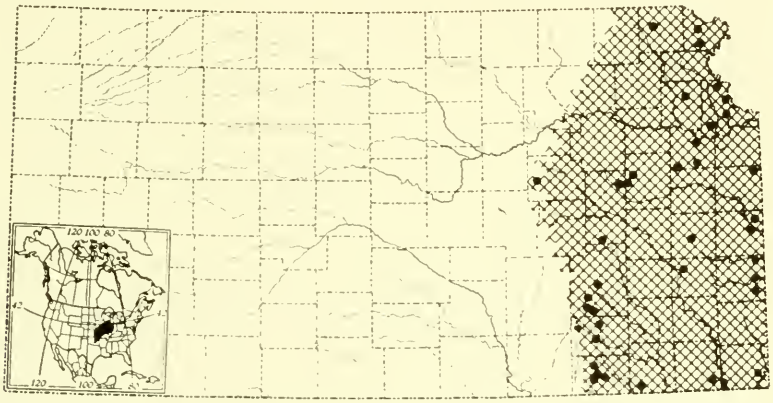

Fig. 3. *Procambarus gracilis*, records in Kansas. Inset shows distribution in North America.

young attached but never with eggs attached. Adults and young appeared in spring and young appeared again in fall. The species was not entirely nocturnal. *Orconectes immunis* was associated with *P. gracilis*. Creaser and Ortenburger (1933:43) stated that *P. gracilis* burrows are often a long distance from surface water and that burrows may be 6 feet deep with an enlarged pocket at the bottom. They reported that females with young had been found in October.

We have collected *P. gracilis*, principally in the spring and fall of the year, from ponds, roadside ditches, burrows in the banks of these bodies of water, from burrows in low wet ground, and have taken juvenile *P. gracilis* from a small creek 12 mi. E Allen, Lyon County, 25 April, 1947. We have never collected females with eggs attached although many of the females have young attached in

early spring. Adult males are rarely found in the daytime, but in early June of 1950 we found form I males abundant at night either at the tops of burrows or wandering overland on low wet ground 2½ mi. SE Lawrence, Douglas County. Young *P. gracilis* are abundant in roadside ditches at this locality in the summer and fall of the year.

RECORDS IN KANSAS

Allen County: Lot 264. 1¾ mi. N Iola; *Anderson County*: Lot 748. Welda; *Bourbon County*: Lot 108. Fulton (SE¼, sec 25, T. 23 S, R. 24 E. & SW¼, sec. 30, T. 23 S, R. 25 E); Lot 110. NW City limits, Ft. Scott (NW¼, sec. 19, T. 25 S, R. 25 E); Lot 113. 9 mi. S Ft. Scott on U. S. 69 (SE¼, SE¼, sec. 18, T. 27 S, R. 24 E); *Brown County*: Lot 156. 7⅒ mi. E Fairview (NE ¼, SE¼, sec. 26, T. 2 S, R. 16 E); *Chautauqua County*: Lot 129. 3½ mi. W Peru (N ½, sec. 24, T. 34 S, R. 11 E); Lot 131. 1½ mi. W, 2½ mi. NW Sedan (NE¼, sec. 29, T. 33 S, R. 11 E); Lot 133. 7½ mi. NW Sedan (NW¼, sec. 31, T. 23 S, R. 11 E); Lot 729. Roadside ditch 2⅒ mi. E Wauneta (sec. 8, T. 34 S, R. 10 E); Lot 732. 5⅒ mi. E Wauneta (sec. 2 & sec. 11, T. 34 S, R. 10 E); *Cherokee County*: Lot 118. Neosho River bottoms 15½ mi. W Baxter Springs (SW¼, sec. 32, T. 35 S, R. 22 E); Lot 260. Crooked Creek, 4 mi. N Riverton (sec. 31, T. 33 S, R. 25 E); *Doniphan County*: Lot 159. 1 mi. E Sparks (SW¼, NE¼, sec. 28, T. 2 S, R. 20 E); Lot 160. 6⅒ mi. SSW Troy (SE¼, NW¼, sec. 11, T. 4 S, R. 20 E); *Douglas County*: Lot 78. 2½ mi. S, ¾ mi. E Snow Hall, Kansas Univ. Lawrence (NE¼, SE¼, sec. 18, T. 13 S, R. 20 E); Lot 81. 1½ mi. S, 3½ mi. W Snow Hall, Kansas Univ., Lawrence (SE¼, sec. 9, T. 13 S, R. 19 E); Lot 85. 12 mi. S Lawrence; Lot 88. 100 yd. SE corner 19th & Illinois St., Lawrence; Lot 97. 1½ mi. N, ½ mi. W Snow Hall, Kansas Univ., Lawrence (NE ¼, SW ¼, & NW¼, SE¼, sec. 25, T. 12 S, R. 19 E); Lot 172. 10⅒ mi. W Junct. U. S. 59 and U. S. 50 (SW¼, SW¼, sec. 36, T. 14 S, R. 17 E); Lot 292. Willow Springs; *Elk County*: Lot 135. 4½ mi. NNE Moline (SE ¼, sec. 23, T. 30 S, R. 10 E); Lot 136. 6 mi. N, ¾ mi. E Howard (NE ¼, sec. 6, T. 29 S, R. 11 E); *Greenwood County*: Lot 136A. ½ mi. N, 2½ mi. W Severy (SE¼, sec. 2, T. 28 S, R. 10 E); Lot 139. 2⅒ mi. N Piedmont (SE¼, sec. 25, T. 27 S, R. 9 E); Lot 141. 7½ mi. SSW Eureka (SE¼, SE¼, sec. 31, T. 26 S, R. 10 E); Lot 142. North city limits, Tonovay (NE¼, NE¼, sec. 27, T. 25 S, R. 11 E); *Jefferson County*: Lot 150. 5⅒ mi. N Oskaloosa (SW¼, sec. 4, T. 9 S, R. 19 E); *Labette County*: Lot 121. 2 mi. W Chetopa (NE¼, sec. 31, T. 35 S, R. 21 E); *Leavenworth*

County: Lot 163. 2⁹⁄₁₀ mi. SE Lovemont (SE ¼, NW¼, sec. 12, T. 8 S, R. 22 E); lot 165. 2 mi. S Lansing (NE¼, sec. 36, T. 9 S, R. 23 E); Lot 167. 4⁹⁄₁₀ mi. S Lansing (SE¼, sec. 13, T. 10 S, R. 23 E); Lot 169. 4 mi. E Junct. U. S. 40 and Kansas 16 at Tonganoxie (SE ¼, sec. 12, T. 11 S, R. 21 E); *Linn County*: Lot 106. 2 mi. N, 2 mi. E Boicourt (NE¼, sec. 19, T. 20 S, R. 25 E); Lot 107. 1¼ mi. SSW Trading Post (SW¼, sec. 8, T. 21 S, R. 25 E); *Lyon County*: Lot 144. 3⁷⁄₁₀ mi. SSE Olpe (SE¼, sec. 23, T. 21 S, R. 11 E); Lot 180. 12 mi. E Allen (SE¼, SE¼, sec. 15, T. 16 S, R. 13 E); *Miami County*: Lot 262. 10 Mile Creek, 1½ mi. S, 2 mi. E Spring Hill; *Montgomery County*: Lot 125. 5 mi. E Caney (NW¼, sec. 11, T. 35 S, R. 14 E); *Morris County*: Lot 187. 22¹⁄₁₀ mi. W Council Grove (SE¼, sec. 8, T. 16, R. 4 E); *Osage County*: Lot 175. 5 mi. S Burlingame (SE¼, SE¼, sec. 3, T. 16 S, R. 14 E); Lot 178. 1 mi. N, 2½ mi. W Osage City (SW¼, sec. 16, T. 16 S, R. 14 E).

KNOWN RANGE

Illinois, Iowa, Kansas, Missouri, Oklahoma, Wisconsin.

REMARKS

Procambarus gracilis has much the same ecological requirements as *P. simulans*. These two species overlap only slightly in their ranges, *P. gracilis* being restricted to the eastern one fourth of the State while *P. simulans* ranges widely over central, western and southern Kansas.

Orconectes neglectus (Faxon)

Plate XCIII and Text fig. 4

Cambarus neglectus Faxon, Bull. Washburn Col. Lab. Nat. Hist., vol. 1, no. 4, 1885, p. 142.
Orconectes neglectus Hobbs, 1942, Amer. Midl. Nat., vol. 28, no. 2, pp. 350-351.

RECOGNITION CHARACTERS

Male form I: (Plate XCIII, fig. F) Rostrum with nearly parallel sides, distinct acumen, poorly defined lateral rostral spines, usually carinate; postorbital ridges each terminating in low, rounded anterior spine; suborbital angle obtuse; cephalothorax ovate, depressed dorsally, punctate dorsally, granulate laterally; cephalic groove interrupted laterally; lateral spine obsolescent; areola wide enough for four rows of punctations at narrowest point, margins poorly defined; head length contained in cephalothorax length 1.49-1.53 times; telson evenly rounded with paired lateral spines; antennae shorter than body, antennal scale (Plate XCIII, fig. G) evenly

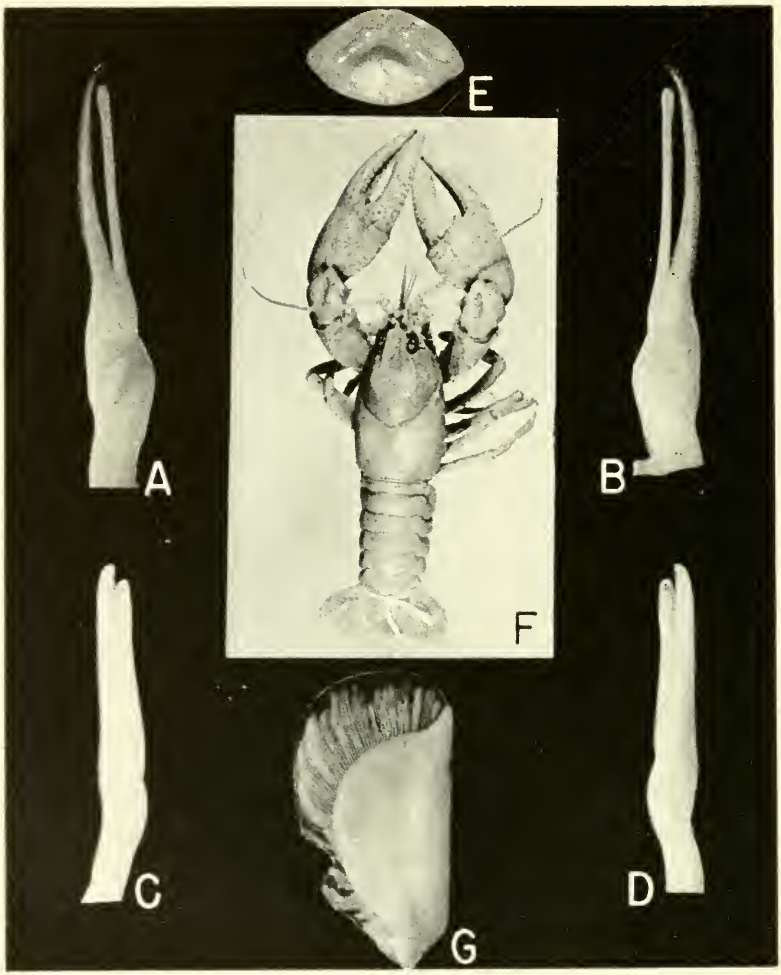

PLATE XCIII

Orconectes neglectus (Faxon)

FIG. A, ♂ form I gonopod, medial view, × 5.
FIG. B, ♂ form I gonopod, lateral view, × 5.
FIG. C, ♂ form II gonopod, medial view, × 5.
FIG. D, ♂ form II gonopod, lateral view, × 5.
FIG. E, Annulus ventralis, × 5.
FIG. F, ♂ form I, × ½.
FIG. G, Antennal scale, × 5.

rounded medially, broadest anterior to midlength, anterior spine moderately developed; chelae heavy, deeply punctate dorsally and ventrally, fingers agape, gape narrower than rostrum at base; medial border of movable finger and palm with double row of flattened tubercles, palm with tendency for development or irregular medial third row; single row of low rounded tubercles on opposed margins of fingers; carpus with two blunt medial spines, anterior one longest; meros with two obsolescent anteapical dorsal spines and a ventral biserial row of irregular obsolescent tubercles, the medial and most anterior of which is spinelike; anterior process of epistoma bell shaped in outline; ischius of third pereiopods with strong hook.

Gonopods end in two elongate nearly straight processes (Plate XCIII, fig. A, B); lateral process (central projection) longer than medial process, corneous with rounded shoulder on cephalic border near base; medial process noncorneous, distal one third flattened, broadened near tip. Tips of processes curve toward each other, reaching base of third pereiopods when abdomen is flexed.

Male form II: Chelae less heavy than in male form I; low tubercle on ischius of third pereiopods; gonopods end in two elongate noncorneous processes separated for only short distance near tips.

Female: Chelae less heavy than in male form I; immovable finger of chelae bearded within near base; annulus ventralis with median transverse sinus dipping under overhanging anterior margin (Plate XCIII, fig. E); annulus divided by sinuous median fossa curving to deepest point on either left or right of midsagittal plane.

Color in life: Ground color a light green to yellow; conspicuous red markings on ridges, tubercles, and tips of chelae; black ring posterior to tips of chelae; black streak on lateral margin of chelae; indefinite black splotches on posterolateral portion of cephalothorax; black markings on pleurae.

Variations: Regenerated chelae relatively longer than normal, fingers not agape.

Ecological Notes

Harris (1902:8) reported *O. neglectus* in the James River near Galloway [Greene County], Missouri. This is a rocky stream with swiftly flowing water. He found *O. neglectus* under loose stones and in vegetation in the water. He also noted that individuals from cold water at the mouth of Galloway Cave [which evidently now bears the name Sequiota Cave and is located on the grounds of the Sequiota State Fish Hatchery in Galloway, Greene County, Missouri] were stiff with cold, and that females there carried eggs

or newly hatched young while those down stream in warmer water had no eggs or young attached. Harris suggested that temperatures there were positively correlated with hatching time. Creaser and Ortenburger (1933:37) noted that *O. neglectus* lives in streams and rivers under rocks and boulders, and that the species seems to prefer streams with clear water and a rather strong current.

We have collected *O. neglectus* from rocky tributaries of the Spring River in Cherokee County, from a spring fed pond and a small overflow stream from this pond at Galena, Cherokee County, and from clear rocky streams near Manhattan, Riley County. The Riley County streams are similar to those in Southeastern Kansas.

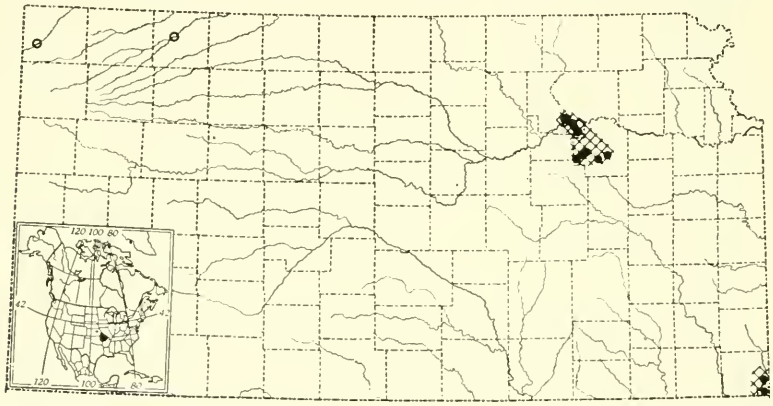

FIG. 4. *Orconectes neglectus*, records in Kansas. Inset shows distribution in North America. Open circles = records from literature.

Many springs flow from limestone outcrops along these stream valleys. The bottom land is cultivated, but the surrounding hill country is untilled range land, so that these streams are not heavily silted. The species apparently prefers to live under rocks in the stream beds, but where clay banks contain the streams both it and *Orconectes nais* have been collected from burrows opening below the surface of the water.

RECORDS IN KANSAS AND COLORADO

Cherokee County: Lot 114. 5 Mile Creek, 6 mi. E Baxter Springs (NE ¼, sec. 1, T. 35 S, R. 25 E); Lot 116. Inside city limits, SW Galena (SW ¼ , sec. 23, T. 34 S, R. 25 E); Lot 256. Turkey Creek, 4 mi. N, ½ mi. E Galena; *Cheyenne County:* Republican River near Guy, [13 mi. SW St. Francis]; *Decatur County:* Sappa Creek, Oberlin; *Riley County:* Lot 242. Wildcat Creek, 3 mi. S, 2½ mi. E

Riley (NW ¼, sec. 20, T. 9 S, R. 6 E); Lot 249. Trib. of Deep Creek, 5 mi. S, 3 mi. E Manhattan (NW ¼, sec. 14, T. 11 S, R. 8 E); Lot 250. Trib. of Deep Creek, 6 mi. S, 3 mi. E Manhattan, (NW ¼, sec. 25, T. 11 S, R. 8 E); Lot 253. Headwaters of Deep Creek, 8 mi. S, 5 mi. E Manhattan (NW ¼, sec. 30, T. 11 S, R. 9 E); *Wabaunsee County:* Lot 769. Mill Creek at Volland (SW ¼, sec. 3, T. 13 S, R. 9 E); Lot 771. Trib. of Mill Creek, 3⅘ mi. SW Volland (NW ¼, sec. 199, T. 13 S, R. 8 E); Lot 773. Trib of Mill Creek, ¾ mi. N Alta Vista (Sec. 35, T. 13 S, R. 8 E); Lot 775. South Branch of Mill Creek, 10 mi. S Alma (sec. 26, T. 13 S, R. 10 E); Lot 777. Mill Creek, 8½ mi. S, 4¼ mi. E Alma (sec. 29, T. 13 S, R. 11 E); *Yuma County, Colorado:* Lot 323. Black Wolf Creek, collected 15 Oct., 1915.

Known Range

"This species is found in the White River drainage in Missouri; Neosho and Grand River drainage in Missouri, Kansas and Oklahoma; Republican River drainage in Kansas and Colorado; and the South Platte River drainage in Colorado. Faxon also records this crayfish from the Red River at Arthur, Lamar County, Texas." (Creaser and Ortenburger 1933:37.)

Remarks

The existing discontinuous distribution of *Orconectes neglectus* within the State is unexplained. The literature indicates that the species had at one time a more widespread distribution within the State than it has at the present. A lot of *O. neglectus* from Black Wolf Creek, Yuma County, Colorado, 15 Oct., 1915, including 1 male form II and 1 female is in the Kansas Univ. Museum of Nat. Hist. Collection. The known distribution of the species is confined to areas where the streams are reasonably clear. Such information leads one to think that increased tillage and consequent increase of silt in streams have been factors restricting the distribution of this species.

Orconectes luteus (Creaser)

Plate XCIV, Text fig. 5

Cambarus juvenilis Hagen [*partim*], 1870, Illinois Cat. Mus. Comp. Zool., no. 3, p. 67.

Cambarus rusticus Faxon [*partim*], 1885, Mem. Mus. Comp. Zool., vol. 10, no. 4, p. 113. Faxon, 1890, Proc. U. S. Nat. Mus., vol. 12, p. 632. Faxon, 1898, Proc. U. S. Nat. Mus., vol. 20, p. 658. Steele, 1902, Pub. Univ. Cincinnati Bull. no. 10, ser. 2, vol. 2, pp. 28-32.

Cambarus rusticus Harris, 1902, Kansas Univ. Sci. Bull., vol. 1, no. 1, p. 8.

Faxonius luteus Creaser, 1933, Occ. Pap. Mus. Zool., Univ. Michigan, no. 275, pp. 7-9, figs. 3-4.

Orconectes luteus Hobbs, 1942, Amer. Midl. Nat., vol. 28, no. 2, pp. 350-351.

RECOGNITION CHARACTERS

Male form I: (Plate XCIV, fig. F) Rostrum widest at base with sides converging to distinct lateral spines, sometimes carinate dorsally, acumen approximately one third as long as rostrum; postorbital ridges each terminate anteriorly in distinct spines; suborbital angle obtuse; cephalothorax ovate, depressed dorsally, punctate dorsally, finely granulate laterally; cephalic groove interrupted laterally; lateral spine small but distinct; areola wide enough for three or four rows of punctations at narrowest part; head length contained in cephalothorax length approximately 1.5-1.6 times; telson evenly rounded, with paired lateral spines; antennae longer than body, antennal scale (Plate XCIV, fig. G) unevenly rounded medially, widest at point anterior to midlength; chelae punctate, double row of flattened tubercles on medial aspect of palm and movable finger; fingers agape, single row of low rounded tubercles on opposed margins of both fingers; carpus with single medial spine and two ventral spines; meros with one, sometimes two distinct dorsal anteapical spines, two distinct anterior spines and an obsolescent biserial row of tubercles ventrally; anterior process of epistoma roughly triangular with distinct but rounded apical point; corneous tipped hooks on ischius of third pair of pereiopods.

Gonopods (Plate XCIV, fig. A, B) terminating in two elongate more or less straight processes, lateral process (central projection) corneous with distinct but rounded shoulder on cephalic border near base, medial process noncorneous, flattened distally; gonopod tips reaching base of third pereiopods with abdomen flexed.

Male form II: Chelae relatively shorter than male form I; hooks on ischius of third pereiopods small, rounded, noncorneous; processes of gonopods (Plate XCIV, fig. C, D) noncorneous, tips closely apposed reaching base of second pereiopods with abdomen flexed.

Female: Chelae relatively smaller than male form I; immovable finger bearded within near base; annulus ventralis with deep transverse sinus bordered anteriorly by elevated margin; annulus (Plate XCIV, fig. E) divided longitudinally by sinous sinus curving to deepest point to right of median sagittal plane.

Color in life: Freshly molted form I male: ground color a light olive green with undertone of yellow on large areas on dorsal side of chelae, rostrum and sides of branchiostegites; dark bandings on posterior margin of head, near articulations of pleurae, dorsal sides of tergae and outer margin of hand; all dorsal tubercles, ridges and

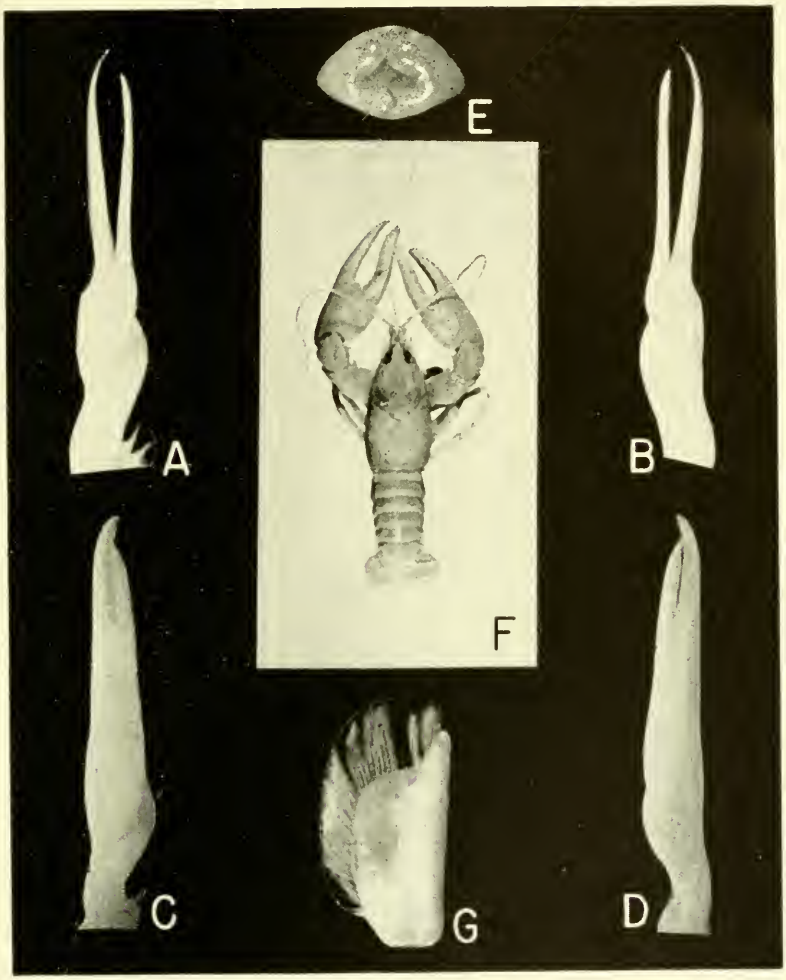

PLATE XCIV

Orconectes luteus (Creaser)

FIG. A, ♂ form I gonopod, medial view, × 5.
FIG. B, ♂ form I gonopod, lateral view, × 5.
FIG. C, ♂ form II gonopod, medial view, × 5.
FIG. D, ♂ form II gonopod, lateral view, × 5.
FIG. E, Annulus ventralis, × 5.
FIG. F, ♂ form I, × ½.
FIG. G, Antennal scale, × 5.

spines brick red; fingers of chelae tipped with brick red, almost scarlet; orange spot on cheeks below eyes; all joints, tubercles and spines on venter vary from light orange to dark orange; underside of hands legs and sternum nearly white; all colors darker in individuals which have not molted recently.

Variations: Regenerated chelae relatively longer than normal; fingers not agape.

Ecological Notes

Creaser (1933:9) stated that *O. luteus* in Missouri lives in clear streams under rocks and that it is found in clear, shallow, swiftly flowing rivers, but not in streams where the bed is muddy or sandy.

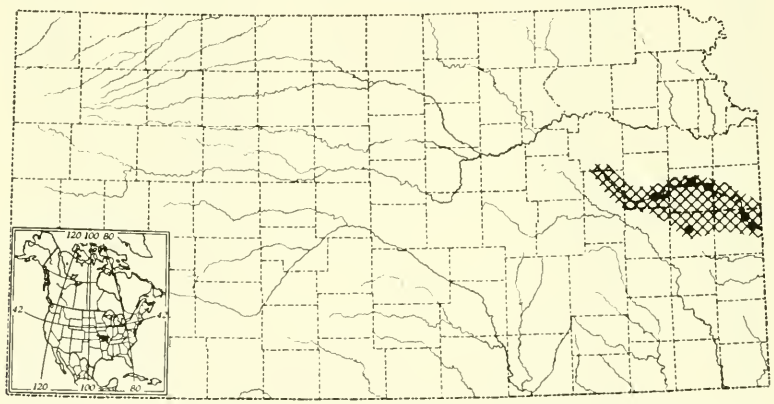

Fig. 5. *Orconectes luteus*, records in Kansas. Inset shows distribution in North America.

We have observed *O. luteus* in streams in the Marais des Cygnes River drainage under similar conditions. However during floods and during normal high water periods these streams carry quantities of silt. *O. luteus* constructs shallow burrows under rocks in the stream bed. We have never found the species in muddy burrows near the edge of streams nor in burrows in mud in the banks of streams. *O. luteus* is commonly associated with *Orconectes nais* in the Marais des Cygnes River.

Records in Kansas

Anderson County: Lot 755. Pottawatomie Creek, 4 mi. N, 4 mi. W Garnett; *Franklin County:* Lot 270. Marais des Cygnes River at Ottawa (NW ¼, sec. 36, T. 16 S, R. 19 E); *Linn County:* Lot 278. Marais des Cygnes River, SW corner LaCygne city limits (NW ¼,

sec. 4, T. 20 S, R. 24 E); Lot 280. Marais des Cygnes River at Trading Post (NW ¼, SE ¼, sec. 5, T. 21 S, R. 25 E); *Osage County:* Lot 273. Long Creek, 2 mi. E Melvern (NW ¼, sec. 12, T. 18 S, R. 16 E).

KNOWN RANGE

Creaser (1933:9) reported that *O. luteus* is found in the headwater streams of the Meramec, Osage, Gasconade, Current and St. Francis river systems in Missouri, and probably less abundantly in these rivers than in the White River drainage. The species is confined to the Marais des Cygnes River drainage in Kansas.

Orconectes nais (Faxon)

Plate XCV, Text fig. 6

Cambarus nais Faxon, 1885, Bull. Washburn Col. Lab. Nat. Hist., vol. 1, no. 4, pp. 140-141.

Cambarus virilis Hagen [*partim*], 1870, Illinois Cat. Mus. Comp. Zool., no. 3, p. 64. Faxon, 1885, Mem. Mus. Comp. Zool., vol. 10, no. 4, pp. 97-98. Faxon, 1890, Proc. U. S. Nat. Mus., vol. 12, p. 630. Faxon, 1898, Proc. U. S. Nat. Mus., vol. 20, p. 652. Faxon, 1914, Mem. Mus. Comp. Zool., vol. 40, no. 8, p. 378. Harris, 1903, Kansas Univ. Sci. Bull., vol. 2, no. 3, pp. 131-135.

Cambarus pilosus Hay, 1899, Proc. U. S. Nat. Mus., vol. 22, pp. 121-122, fig. 1.

Cambarus pelosus [*sic*] Harris, 1901, Trans. Kansas Acad. Sci., vol. 17, p. 115.

Cambarus virilis Hagen, Harris, 1900, Kansas Univ. Quart., vol. 9, ser. 2, pp. 269-270. Harris, 1901, Trans. Kansas Acad. Sci., vol. 17, p. 115. Harris, 1902, Kansas Univ. Sci. Bull., vol. 1, no. 1, p. 6. Steele, 1902, Pub. Univ. Cincinnati Bull. no. 10, ser. 2, vol. 2, p. 32, pls. 1-2. Engle, 1926, Bull. Bur. Fish., vol. 42, p. 91.

Orconectes nais Hobbs, 1942, Amer. Midl. Nat., vol. 28, no. 2, pp. 350-351.

RECOGNITION CHARACTERS

Male form I: (Plate XCV, fig. F) Rostrum widest at base, sides converging to weakly developed lateral spines, acumen distinct, dorsal excavation deepest near rostral base; postorbital ridges each terminate in low anterior spine; suborbital angle obtuse; cephalothorax ovate, sparsely punctate dorsally, granulate laterally; cephalic groove interrupted laterally, distinct lateral spine; areola width allowing single row of punctations at narrowest point, margins parallel at midlength; head length contained in cephalothorax length approximately 1.49-1.56 times; telson evenly rounded, with paired lateral spines; antennae longer than body, antennal scale (Plate XCV, fig. G) unevenly rounded medially, widest at midlength with moderately developed apical spine; chelae punctate, fingers emarginate, slight gape at base of fingers, double row of raised tubercles on medial aspect of palm and movable finger, immovable finger bearded within near base, single row of raised tubercles on opposed margins of fingers with single nearly opposed enlarged tubercles in

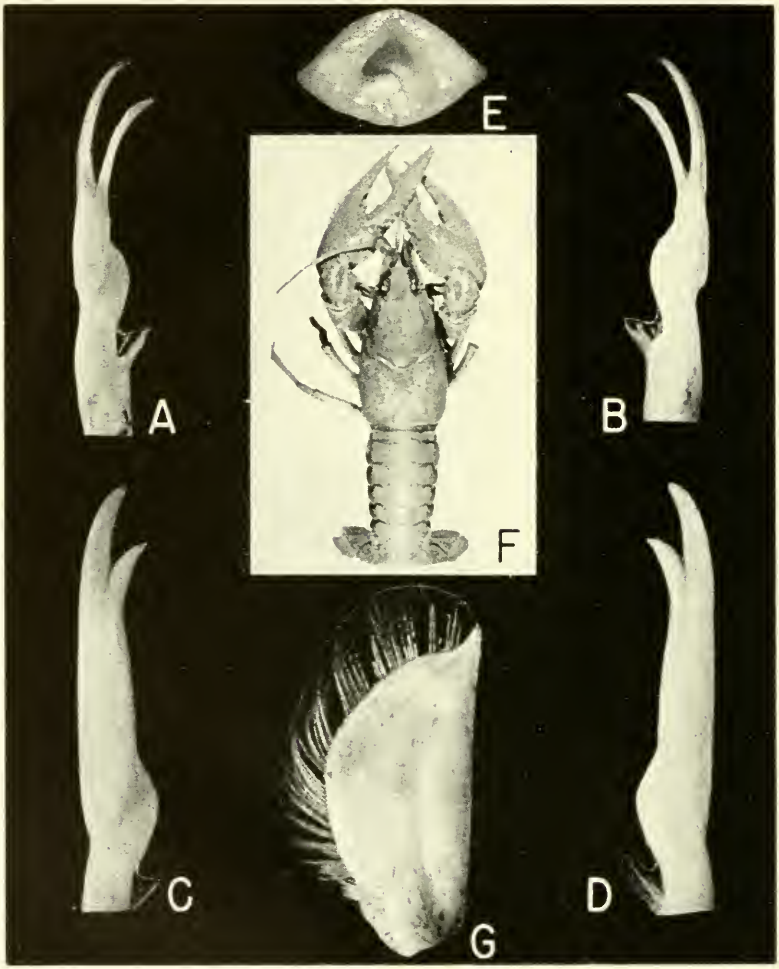

PLATE XCV

Orconectes nais (Faxon)

FIG. A, ♂ form I gonopod, medial view, × 5.
FIG. B, ♂ form I gonopod, lateral view, × 5.
FIG. C, ♂ form II gonopod, medial view, × 5.
FIG. D, ♂ form II gonopod, lateral view, × 5.
FIG. E, Annulus ventralis, × 5.
FIG. F, ♂ form I, × ½.
FIG. G, Antennal scale, × 5.

proximal ¼ of row on both fingers; carpus with two sharp medial spines, most anterior largest, two to three moderately sharp spines ventrally; meros with one to two dorsal anteapical spines, ventral biserial row of spines with distal spines most strongly developed; anterior process of epistoma nearly rounded anteriorly; ischius of third pereiopods with hooks.

Gonopods (Plate XCV, fig. A, B) ending in two elongate processes, both processes gently curved caudad at tips to angle considerably less than 90° with axis of shaft, lateral process (central projection) corneous, longer than medial process, medial process noncorneous; both processes bladelike at tips, tips reach to base of second pereiopods with abdomen flexed.

Male form II: Chelae not as heavy as male form I; greatly reduced hooks on ischius of third pereiopods; gonopods (Plate XCV, fig. C, D) ending in two noncorneous processes separated through distal one fourth of length, tips closely apposed, lateral process the longest.

Female: Chelae not so heavy as male form I; annulus ventralis with deep median sinus in anterior half, deepest portion either to right or left of mid-sagittal plane; annulus (Plate XCV, fig. E) divided by sinuous median sinus curving into deepest portion of sinus.

Color in life: Body green to dull rusty reddish brown dorsally; chelae green, blue or bluish green dorsally, with scattered bright yellow to orange tubercles especially on cutting edges of fingers and along margins; eggs apparently black; freshly molted individuals light green.

Variations: Most of the male form I specimens collected from the State appear to have longer, less curved gonopods than the cotypes of *O. nais* in the Kansas Univ. Mus. Nat. Hist. collection. However form I males in Lot 109, Bourbon County, have gonopods in which the fleshy processes are strongly recurved caudad throughout their length, while specimens in the lots from Moline River drainage in Elk County, have gonopods similar to the cotypes. Sculpture of the annulus shows individual variations. Configuration of the median edge of the antennal scale also shows individual variations.

ECOLOGICAL NOTES

Harris (1900:269) reported *O. nais* from a spring-fed rocky stream in Labette County, (1902:7) from a "wet weather" stream in the central part of the State, and from a well five feet deep near this stream. Harris (1903:118) observed the species burrowing un-

der grass tussocks at the edge of a small stream. The burrows were about two feet long, branched and under water. Creaser and Ortenburger (1933:38) reported *O. nais* from a wide range of habitats from slowly moving to swiftly moving water.

We have found this species in ponds, streams and ditches, and under conditions in which the water was both relatively free of submerged vegetation and debris, or in situations in which the water was choked with such materials. The species is apparently not primarily a burrowing species, but lives in open water, under

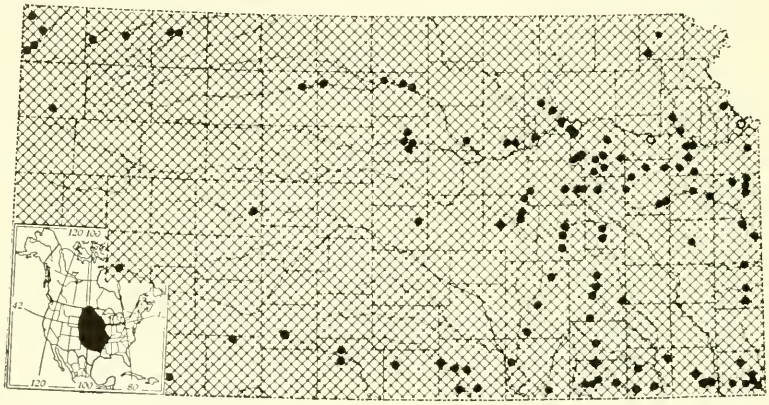

FIG. 6. *Orconectes nais*, records in Kansas. Inset shows distribution in North America. Open circles = records from literature.

rocks, or at times in burrows in the muddy or clayey banks of streams. These crayfishes are not abundant in sandy streams, nor in extremely muddy stagnant ditches or ponds. Old individuals tend to stay in burrows or under other types of cover during the day. They forage mostly at night. Young individuals may be found in open water during either the day or night. *Orconectes nais* is commonly associated with *O. luteus* and *O. neglectus* where these species occur and less commonly with *O. immunis* and *Cambarus diogenes, Procambarus gracilis* and *P. simulans.*

RECORDS IN KANSAS

Anderson County: Lot 736. 4 mi. S Garnett (sec. 19, T. 21 S, R. 20 E); *Barber County:* Lot 89. 4⅗ mi. S Sun City; Lot 317. 1½ mi. N Sun City (sec. 25, T. 30 S, R. 15 W); *Bourbon County:* Lot 109. Fulton (SE ¼, sec. 25, and the SW ¼, sec. 30, T. 23 S, R. 25 E); Lot 111. NW city limits, Ft. Scott (NW ¼, sec. 19, T. 25 S, R. 25 E); Lot 112. 9 mi. S Ft. Scott on U. S. 69 (SE ¼, SE ¼, sec.

18, T. 27 S, R. 24 E); *Brown County:* Lot 154. 9⅘ mi N Netawaka (NE ¼, sec. 4 and the NW ¼, sec. 3, T. 4 S, R. 15 E); Lot 155. Spring Creek, 2⅘ mi. E Fairview (S ½, sec. 25 and the N ½, sec. 36, T. 2 S, R. 15 E); Lot 158. 7⅘ mi E Fairview (NE ¼, SE ¼, sec. 26, T. 2 S, R. 16 E); *Butler County:* Lot 298. 7 mi. N, 5 mi. E Eldorado (sec. 4, T. 24 S, R. 6 E); Lot 299. Spring Cave, 7 mi. S Eldorado; Lot 301. 2⅘ mi. S Douglass (sec. 35, T. 29 S, R. 4 E); *Chase County:* Lot 293. 1½ mi. SE Strong City (sec 22, T. 19 S, R. 8 E); Lot 294. 2⅘ mi. S Cottonwood Falls (NE ¼, sec. 8, T. 20 S, R. 8 E); Lot 295. 7 mi. S, ½ mi. W Cottonwood Falls (sec. 32, T. 20 S, R. 8 E); Lot 296. Baker Creek, 11 mi. S, 1 mi. W Cottonwood Falls (E ½, sec. 19, T. 21 S, R. 8 E); *Chautauqua County:* Lot 127. Davis Creek, 1½ mi. WNW Niotaze (SE ¼, sec. 24, T. 34 S, R. 12 E); Lot 130. ½ mi. W, 2½ mi. NW Sedan (NE ¼, sec. 29, T. 33 S, R. 11 E); Lot 132. 7½ mi. NW Sedan (NW ¼, sec. 31, T 23 S, R. 11 E); Lot 728. Shanghi Creek, ½ mi. W Wauneta (sec. 11, T. 34 S, R. 9 E); Lot 731. Roadside ditch, 2⅘ mi. E Wauneta (sec. 8, T. 34 S, R. 10 E); Lot 733. 5⅘ mi. E Wauneta (sec. 2 and sec. 11, T. 34 S, R. 10 E); *Cherokee County:* Lot 61. Brush Creek on Hy. 32; Lot 63. ¼ mi. S, 1 mi. W Jayhawk Ordnance Plant; Lot 115. ½ mi. N Baxter Springs (NW ¼, sec. 36, T. 35 S, R. 24 E); Lot 117. 4 Mile Creek, 6 mi. W Baxter Springs (SW ¼, sec. 32, T. 35 S, R. 23 E); Lot 255. Crooked Creek, 3 mi. N Riverton; Lot 258. Shoal Creek, 3 mi. S, 2½ mi. W Galena; *Cheyenne County:* Lot 212. Republican River bottoms, 13 mi. SW St. Francis (sec. 34, T. 4 S, R. 42 W); Lot 213. Crosby Creek, 7 mi. SW St. Francis (SW ¼, sec. 11, T. 4 S, R. 41 W); Lot 214. Hackberry Creek, 15 mi. NW St. Francis (W ½, sec. 4, T. 2 S, R. 41 W); Lot 215. Cherry Creek, ½ mi. N, ½ mi. W St. Francis (SW ¼, sec. 6, T. 3 S, R. 40 W); *Clark County:* Lot 90. Bluff Creek, Pyle Ranch, 4 mi. S Kingsdown; *Cowley County:* Lot 302. 6 mi. W Winfield (sec. 20, T. 32 S, R. 3 E); Lot 727. Panther Creek, 13⅘ mi. ENE Arkansas City (sec. 18, T. 34 S, R. 6 E); *Decatur County:* Lot 218. Trib. of Oberlin Lake, 1 mi. NW Oberlin (SW ¼, SW ¼, sec. 30, T. 32 S, R. 28 W); Lot 219. Sappa Creek, 1½ mi. N, 2 mi. E Oberlin (SW ¼, sec. 28, T. 2 S, R. 28 W); *Dickinson County:* Lot 238. Mud Creek, 7 mi. N, 1 mi. W Abilene (SE ¼, sec. 1, T. 12 S, R. 1 E); Lot 239. 8 mi. N Enterprise (NE ¼, sec. 9, T. 12 S, R. 3 E); *Douglas County:* Lot 57. W branch of Ottawa Creek, 16 mi. S, ¼ mi. E Lawrence; Lot 71. 1½ mi. S, 3½ mi. W Snow Hall, Kansas Univ., Lawrence

(SE ¼, sec. 9, T. 13 S, R. 19 E); Lot 72. 3 mi. S, 2¾ mi. W Snow Hall, Kansas Univ., Lawrence (NW ¼, sec. 22, T. 13 S, R. 19 E); Lot 73. 2½ mi. S, 1¼ mi. E Snow Hall, Kansas Univ., Lawrence (NW ¼, sec. 17, T. 13 S, R. 20 E); Lot 98. 5 mi. W Snow Hall, Kansas Univ., Lawrence (SW ¼, sec. 32, T. 12 S, R. 18 E); Lot 171. 10⅘ mi. W Junct. U. S. 59 and U. S. 50 (SW ¼, SW¼, sec. 36, T. 14 S, R. 17 E); Lot 269. 12 mi. S Lawrence (SE ¼, sec. 2, T. 15 S, R. 19 E); Lot 745. 14 mi. S, 1 mi. W Lawrence; Lot 746. Lone Star Lake [8 mi. S, 8 mi. W, Lawrence]; *Elk County:* Lot 134. 4½ mi. NNE Moline (SE ¼, sec. 23, T. 30 S, R. 10 E); Lot 135A. 6 mi. N, ¾ mi. E Howard (NE ¼, sec. 6, T. 29 S, R. 11 E); *Finney County:* Lot 10. Garden City; *Franklin County:* Lot 271. Marais des Cygnes River at Ottawa (NW ¼, sec. 30, T. 18 S, R. 19 E); Lot 276. Marais des Cygnes River, 1¾ mi. N Rantoul (NW ¼, sec. 16, T. 17 S, R. 21 E); *Geary County:* Lot 240. Republican River bottoms, 1⅘ mi. NW Junction City (E ½, sec. 27, T. 12 S, R. 5 E); *Greenwood County:* Lot 55. S branch, Carlyle Creek, Hibbard Ranch, 8 mi. SW Toronto; Lot 137. 1 mi. N, 1 mi. W Piedmont (SE ¼, SE ¼, sec. 2, T. 28 S, R. 9 E); Lot 138. 2⅗ mi. N Piedmont (SE ¼, sec. 25, T. 27 S, R. 9 E); Lot 140. 7½ mi. SSW Eureka (SE ¼, SE ¼, sec. 31, T. 26 S, R. 10 E); Lot 143. North city limits, Tonovay (NE ¼, NE ¼, sec. 27, T. 25 S, R. 11 E); Lot 146. Bernard Creek, 4 mi. N Tonovay (NE ¼, NE ¼, sec. 3, T. 25 S, R. 11 E); *Harper County:* Lot 312. Middle Branch, Bluff Creek, 3¼ mi E Attica (sec. 23, T. 32 S, R. 8 W); *Jefferson County:* Lot 1. Wild Horse Creek; Lot 76. 1¼ mi. NE Williamstown (NW ¼, NE ¼, sec. 20, T. 11 S, R. 19 E); *Johnson County:* Lot 101. 13½ mi. S Junct. Kansas 10 and U. S. 69 (SE ¼, sec. 19, T. 14 S, R. 25 E); *Kiowa County:* Lot 751. Spring at head of Medicine Lodge River, S of Greensburg; *Labette County:* Lot 12. Labette Creek; Lot 29. Labette County (TYPES); Lot 120. 2 mi. W Chetopa (NE ¼, sec. 31, T. 35 S, R. 21 E); Lot 122. Turkey Creek, 4 mi. W Chetopa (SE ¼, sec. 26, T. 34 S, R. 20 E); *Leavenworth County:* Lot 164. 2 mi. S Lansing (NE ¼, sec. 36 and the NW ¼, sec. 3, T. 9 S, R. 23 E); *Lincoln County:* Lot 5. Saline River; Lot 228. 9 mi. N Lincoln (NW ¼, sec. 19, T. 10 S, R. 7 W); Lot 230. 5⅗ mi. N Lincoln (NW ¼, sec. 6, T. 11 S, R. 7 W); Lot 231. Beaver Creek, ½ mi. S, 2 mi. E Lincoln (SW ¼, sec. 4, T. 12 S, R. 7 W); *Linn County:* Lot 279. Marais des Cygnes River, SW corner of La Cygne city limits (NW ¼, sec. 4, T. 20 S, R. 24 E); Lot 281. 2½ mi. N Trading Post

(SE ¼, sec. 19, T. 20 S, R. 25 E); *Lyon County:* Lot 145. 3⅞ mi. SSE Olpe (SE ¼, sec. 23, T. 21 S, R. 11 E); Lot 148. 5½ mi. S Emporia (W ½, sec. 15, T. 20 S, R. 11 E); Lot 179. 12 mi. E Allen (SE ¼, SE ¼, sec. 15, T. 16 S, R. 13 E); Lot 181. Hill Creek, 1¾ mi. E Allen (SE ¼, sec. 13, T. 16 S, R. 11 E); *Marion County:* Lot 188. 1 mi. E Lost Springs (NW ¼, NW ¼, sec. 24, T. 17 S, R. 4 E); Lot 189. Clear Creek, 1½ mi. S Lincolnville (SE ¼, sec. 23, T. 18 S, R. 4 E); Lot 190. East Creek, 3⅛ mi. S Lincolnville (NW ¼, sec. 2, T. 19 S, R. 4 E); Lot 191. 7⅞ mi. S Lincolnville (NW ¼, sec. 22, T. 19 S, R. 4 E); Lot 193. 1 mi. N, 2 mi. W Hillsboro (NE ¼, sec. 31, T. 19 S, R. 2 E); *Meade County:* Lot 60. Meade County State Lake, 14 mi. SW Meade; *Miami County:* Lot 56. Little Bull Creek, 4 mi SW Spring Hill; Lot 102. 4 mi. N, ¼ mi. E Louisburg (NW ¼, sec. 5, T. 16 S, R. 25 E); Lot 103. 1½ mi. N Louisburg (NW ¼, sec. 20, T. 16 S, R. 25 E); Lot 104. 3 mi. S Louisburg (SW ¼, sec. 17 and the SE ¼, sec. 18, T. 17 S, R. 25 E); Lot 261. 10 Mile Creek, 2 mi. E, 1½ mi. S Spring Hill; *Mitchell County:* Lot 3. Beloit; Lot 222. Granite Creek, 2¾ mi. E Cawker City (SW ¼, sec. 19, T. 6 S, R. 9 W); Lot 223. Brown Creek, 1 mi. S, 5 mi. E Glen Elder (NW ¼, sec. 3, T. 7 S, R. 8 W); *Montgomery County:* Lot 30. Branch of Coal Creek; Lot 123. Spring Creek, 4 mi. W Coffeyville (NE ¼, sec. 1, T. 35 S, R. 16 E); Lot 126. 5 mi. E Caney (NW ¼, sec. 11, T. 35 S, R. 14 E); Lot 734. Cherry Creek, 1⅞ mi. N Cherryvale (sec. 33, T. 31 S, R. 17 E); *Morris County:* Lot 182. 7 mi. E Council Grove (SW ¼, sec. 12, T. 16 S, R. 9 E); Lot 183. 4 mi. E Council Grove (SE ¼, SE ¼ sec. 9, T. 16 S, R. 9 E); Lot 184. 1½ mi. E Council Grove (SE ¼, sec. 17, T. 16 S, R. 9 E); Lot 185. 6⅜ mi. W Council Grove (SE ¼, sec. 14, T. 16 S, R. 7 E); Lot 186. 22⅛ mi. W Council Grove (SE ¼, sec. 8, T. 16 S, R. 4 E); *Neosho County:* Lot 263. 5 mi. W St. Paul; Lot 735. Neosho River, 2 mi. N Chanute (sec. 4, T. 27 S, R. 18 E); *Ness County:* Lot 208. Walnut Creek, 2¾ mi. E Bazine (SW ¼, sec. 28, T. 18 S, R. 21 W); *Osage County:* Lot 173. ½ mi. E Overbrook (S ½, sec. 32, T. 14 S, R. 17 E); Lot 174. 110 Mile Creek, 1½ mi. E Scranton (SE ¼, sec. 35, T. 14 S, R. 15 E); Lot 176. 5 mi. S Burlingame (SE ¼, SE ¼, sec. 3, T. 16 S, R. 14 E); Lot 177. 1 mi. N, 2½ mi. W Osage City (SW ¼, sec. 16, T. 16 S, R. 14 E); Lot 272. Trib. Marais des Cygnes River, 6 mi. E Melvern (S ½, sec. 5, T. 18 S, R. 17 E); Lot 274. Long Creek, 2 mi. E Melvern (NW ¼, sec.

12, T. 18 S, R. 16 E); Lot 275. Marais des Cygnes River, ½ mi. N Melvern (NE ¼, sec. 4, T. 18 S, R. 16 E); *Osborne County:* Lot 221. 3½ mi. W Alton (S ½, sec. 7, T. 7 S, R. 15 W); *Ottawa County:* Lot 234. E branch of Coal Creek, 6¼ mi. E Bennington (N ½, sec. 7, T. 12 S, R. 1 W); *Rawlins County:* Lot 216. Little Beaver Creek, 2 mi S, 1 mi. E Beardsley (NW ¼, NW ¼, sec. 24, T 3 S ,.R. 35 W); Lot 217. Beaver Creek, 1 mi. N, 3 mi. E Atwood (NE ¼, sec. 3, T. 3 S, R. 33 W); *Rice County:* Lot 199. Little Arkansas River, 2 mi. N, 10½ mi. E Lyons (SW ¼, sec. 21, T. 19 S, R. 6 W); *Riley County:* Lot 7. 2 mi. W Manhattan; Lot 241. Wildcat Creek, SW corner Riley city limits (SW ¼, sec. 2, T. 9 S, R. 4 E); Lot 243. Wildcat Creek, 3 mi. S, 2½ mi. E Riley (NW ¼, sec. 20, T. 9 S, R. 6 E); Lot 244. Silver Creek, ½ mi. W Keats (S ½, sec. 36, T. 9 S, R. 6 E); Lot 245. 1½ mi. NE Keats (W ½, sec. 30, T. 9 S, R. 7 E); Lot 247. Trib. of Deep Ceek, 3½ mi. S, 4 mi. E Manhattan (NW ¼, sec. 1, T. 11 S, R. 8 E); Lot 252. Headwaters of Deep Creek, 8 mi S, 5 mi. E Manhattan (NW ¼, sec. 30, T. 11 S, R. 9 E); *Rooks County:* Lot 220. 1¾ mi. W Woodson (NW ¼, sec. 17, T. 7 S, R. 16 W); *Shawnee County:* Wards Creek; *Sherman County:* Lot 211. N Smoky Hill River, 10 mi. S, 1 mi. W Goodland (sec. 13, T. 10 S, R. 40 W); *Sumner County:* Lot 306. 6 mi. W Wellington (sec. 22, T. 32 S, R. 2 W); Lot 308. Sand Creek, 2 mi. W Milan (sec. 23, T. 32 S, R. 4 W); Lot 310. Chickaskia Creek, ¼ mi. N, 1½ mi. W Argonia (sec. 7, T. 32 S, R. 4 W); Lot 726. Spring Creek, Junct. U. S. 81 & U. S. 166 at South Haven (sec. 26, T. 34 S, R. 1 W); *Wabaunsee County:* Lot 723. Johnson Creek, 3⁶⁄₁₀ mi. WSW Dover (sec. 21, T. 13 S, R. 13 E) in Wabaunsee County; Lot 724. Trib. of Rock Creek, 11½ mi. SW Eskridge (SW ¼, sec. 25, T. 14 S, R. 10 E); Lot 725. Rock Creek, 16 mi. SW Eskridge (NW ¼, sec. 10, T. 15 S, R. 10 E); Lot 770. Mill Creek at Volland (SW ¼, sec. 3, T. 13 S, R. 9 E); Lot 772. Trib. of Mill Creek, 3⁹⁄₁₀ mi. SW Volland (NW ¼, sec. 19, T. 13 S, R. 8 E); Lot 774. Trib. of Mill Creek, ¾ mi. N Alta Vista (sec. 35, T. 13 S, R. 8 E); Lot 776. South Branch of Mill Creek, 10 mi. S Alma (sec. 26, T. 13 S, R. 10 E); Lot 778. Mill Creek, 8½ mi. S, 4¼ mi. E Alma (sec. 29, T. 13 S, R. 11 E); Lot 779. Trib. of Mill Creek, ½ mi. S, ¾ mi. W Paxico (sec. 27, T. 11 S, R. 11 E); *Wyandotte County:* Small stream near Edgerton.

KNOWN RANGE

According to Creaser and Ortenburger (1933:38) the range of *O. nais* is the Great Plains area and the Ozark region, west of the Mississippi River.

REMARKS

The distinction between *Orconectes nais* and a closely related species, *O. virilis,* which occurs in the northern and eastern Mississippi Valley drainage has long been a subject of confusion. The exact limits of the ranges of these two species is not known.

Orconectes immunis (Hagen)

Plate XCVI, Text fig. 7

Cambarus immunis Hagen, 1870, Ill. Cat. Mus. Comp. Zool., no. 3, p. 71, pl. 1, figs. 101-102, pl. 3, fig. 160, pl. 8, fig. b.
Cambarus signifer Herrick, 1882, 10th Ann. Rpt. Geol. Surv. Minnesota, p. 253.
Cambarus immunis spinirostris Faxon, 1884, Proc. Amer. Acad. Arts and Sci., vol. 20, p. 146.
Faxonius immunis immunis Creaser, 1933, Occ. Pap. Mus. Zool., Univ. Michigan, no. 275, p. 13.
Faxonius immunis pedianus Creaser, *Ibid.,* p. 302.
Faxonius immunis pedianus Fleming, 1939, Jour. Tennessee Acad. Sci., vol. 14, no. 3, 1939, p. 302.
Orconectes immunis immunis Hobbs, 1942, Amer. Midl. Nat., vol. 28, no. 2, p. 350. Hobbs and Marchand, 1943, Jour. Tennessee Acad. Sci., vol. 18, no. 1, p. 24, pl. 2, figs. 4, 8, pl. 3, figs. 18, 25. Rhoades, 1944, Amer. Midl. Nat., vol. 31, no. 1, p. 132.

RECOGNITION CHARACTERS

Male form I: (Plate XCVI, fig. F) Rostrum longer than broad, reaching cephalad to anterior tips of antennal scales, excavated dorsally, lateral rostral spines indistinct or absent; postorbital ridges nearly straight, terminating anteriorly in blunt spines; suborbital angle acute; cephalothorax ovate, punctate dorsally, cephalic portion punctate laterally, thoracic portion granulate laterally; cephalic groove interrupted laterally, short sharp lateral spines present; areola narrowest in anterior half of length, wide enough for one row of punctations at narrowest point; areola length contained in head length approximately 1.70-2.31 times; telson evenly rounded caudally with paired lateral spines; antennae longer than cephalothorax; antennal scale (Plate XCVI, fig. G) unevenly rounded medially, widest near mid-length, truncate at apex, terminal spine small; chelae slender, punctate, tuberculate along medial margin of palm and movable finger, opposed edges of fingers with single row of rounded tubercles, large opposed tubercles in proximal half of rows, immovable finger bearded within near base; carpus

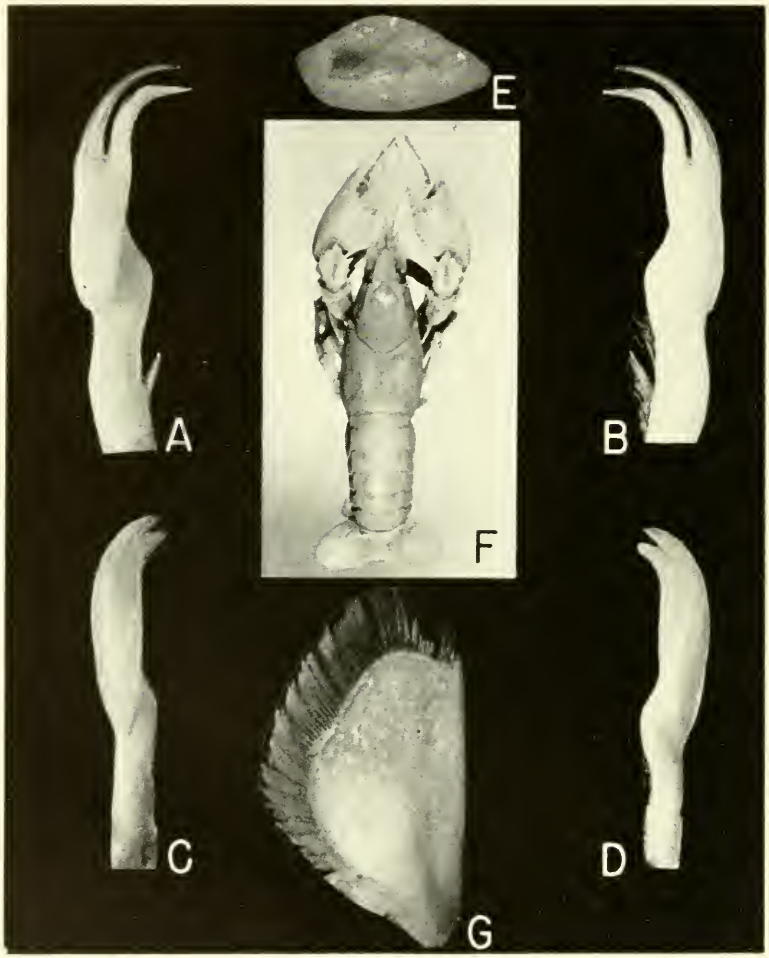

PLATE XCVI

Orconectes immunis (Hagen)

FIG. A, ♂ form I gonopod, medial view, × 5.
FIG. B, ♂ form I gonopod, lateral view, × 5.
FIG. C, ♂ form II gonopod, medial view, × 5.
FIG. D, ♂ form II gonopod, lateral view, × 5.
FIG. E, Annulus ventralis, × 5.
FIG. F, ♂ form I, × ½.
FIG. G, Antennal scale, × 5.

with one large sharp spine and several small spines medially, one prominent median ventral spine; anterior process of epistoma triangular, margins finely and irregularly toothed; ischius of third pereiopods with strongly pointed hooks.

Gonopods (Plate XCVI, fig. A, B) terminating in two elongate processes, tips of processes bent at approximately 90° angle to axis of shaft, lateral process (central projection) corneous; medial process noncorneous, excavated on cephalic border; tips of gonopods reach base of third pereiopods with abdomen flexed.

Male form II: Chelae less heavily developed than male form I; hooks on ischius of third walking legs with rounded apex, processes of gonopods (Plate XCVI, fig. C, D) thick, noncorneous, tips closely apposed.

Female: Chelae proportionately smaller than male form I; annulus ventralis with deepest portion of sinus displaced to right or left of midsagittal plane, sculpture variable.

Color in life: Ground color olive green, first segment may show light tinge of red dorsally; appendages with pinkish hue; chromatophores on dorsal side form irregularly shaped symmetrical pattern in freshly molted individuals; eggs of young females brownish red, eggs of old females darker.

Life History and Ecology

According to Forbes (1876:4) *Orconectes immunis* was the commonest species of crayfish in central Illinois and was especially abundant in muddy ponds. Harris (1903:103) found *O. immunis* in roadside ditches and stagnant ponds. He also reported that *O. immunis* was associated with *Procambarus gracilis* and *Orconectes* [*nais*] in some of these ponds. Creaser and Ortenburger (1933: 38) stated that *Orconectes immunis* prefers slowly moving streams, ponds, or lakes with muddy bottoms and with an abundance of vegetation. Tack (1941:422-427) published his findings on the life history and ecology of *O. immunis* based on a study of this species where it occurs at Ithaca, [Tompkins County,] New York. The mud bottoms of fish ponds at the Cornell Experimental hatchery contained many *Orconectes immunis,* but a nearby small stream "with rubble bottom and a moderate current" contained few specimens of *O. immunis.* Our own observations in Kansas indicate that this species apparently has a preference for roadside ditches, ponds and small sluggish mud-bottomed streams. Harris (1903:103) described the species as a "burrowing and at least to a certain extent a chimney building species" and he cited observations on chimneys

built by the species. Tack reported that burrows are usually near the surface of the water and are directed horizontally into the bank with a deeper cell at the end of the burrow. He stated that several individuals may occupy a depression or burrow under the edge of the turf and he found that the burrows are seldom more than 14 inches deep, although they sometimes reached a depth of 21 inches. When the ponds at the Cornell Experimental hatchery were drained, about half of the crayfishes followed the water and half burrowed through the mud in the pond bottom to underlying gravel where they remained until the pond was refilled. Tack

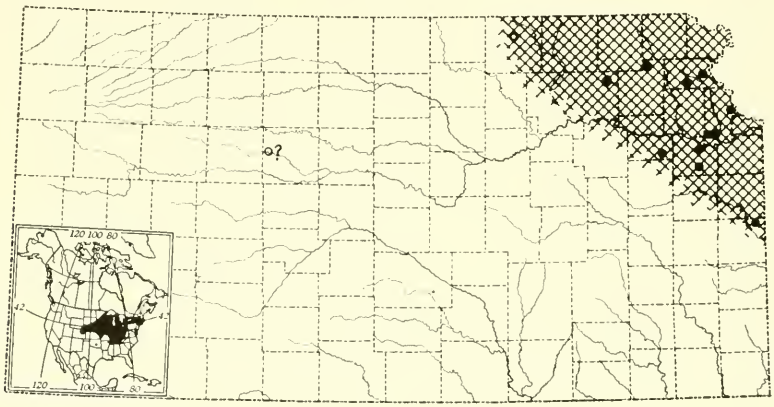

FIG. 7. *Orconectes immunis*, records in Kansas. Inset shows distribution in North America. Open circles = records from literature.

recorded only one chimney construction observed during his four year study of *O. immunis*, but mentioned that burrows constructed at times of low water were sealed with pellets of mud. Harris (1903:105) stated that the shaft of the burrow usually went straight down but sometimes was quite sinuous and more than 4 feet deep. The animals, according to him, usually rested above the water level in the burrow. The burrows in his opinion served as a retreat in dry weather, but did not seem to be used as retreats while the eggs were being hatched.

Tack noted that the greatest activity of *O. immunis* is at night. He found that young crayfishes during their first summer are active both day and night until autumn, while the greatest activity among adults was predominantly nocturnal. He observed that young crayfishes leave the aquatic vegetation and shallow water at the close of their first summer. They retire to deeper water along with the adults and seek cover in burrows or under stones for the dura-

tion of the winter. "Only at night do crayfish leave the ponds to migrate across the banks to other ponds. They move about on the banks considerably during the summer, particularly when the grass is wet with dew or rain." Tack regarded this behavior as further evidence that crayfishes are primarily nocturnal.

Engle (1926:97) found two females in berry near Lincoln, [Lancaster County] Nebraska on April 25. One specimen taken on October 30 had eggs which were hatching. Creaser and Ortenberger (1933:38) reported females with eggs from Fargo [Cass County,] North Dakota on June 6.

Distribution in Kansas

Atchison County: Lot 151. South Stranger Creek, 4½ mi. S, 1 mi. W Monrovia (NW ¼, NW ¼, sec. 12, T. 7 S, R. 18 E); Lot 161. 8 mi. SW Atchison (NW ¼, sec. 30, T. 6 S, R. 20 E); Lot 162. 7 mi. SW Atchison (SE¼, sec. 20 and the NE ¼, sec. 29, T. 6 S, R. 20 E); *Douglas County:* Lot 70. 2 mi. S, ¾ mi. E (NE ¼, sec. 18, T. 13 S, R. 20 E); *Ellis County:* Ellis; *Jackson County:* Lot 153. 2 7/10 mi. SSW Netawaka (SE ¼, NE ¼, sec. 33, T. 5 S, R. 15 E); *Leavenworth County:* Lot 166. 2 mi. S Lansing (NW ¼, sec. 3, T. 9 S, R. 23 E); Lot 168. 4 mi. E Junct. U. S. 40 and Kansas 16 at Tonganoxie (SE ¼, sec. 12, T. 11 S, R. 21 E); Lot 170. 1 mi. E Tonganoxie (SE ¼, sec. 10, T. 11 S, R. 21 E); *Linn County:* Lot 105. 2 mi. N, 2 mi. E Boicourt (NE ¼, sec. 19, T. 20 S, R. 25 E); *Pottawatomie County:* Lot 15. Onaga; *Shawnee County:* Lot 19. Ward's Creek; *Washington County:* Washington County.

Known Range

The range of this species, according to Creaser (1933:15), is from Massachusetts to Wyoming and from Tennessee to Ontario, but the exact extent of the range is not known.

Remarks

The taxonomic status of *Orconectes immunis* has been in a confused state for many years. Creaser (1933:13) recognized an eastern and a western subspecies (*O. immunis immunis* and *O. immunis pediamus* respectively). He based the distinctions between the two subspecies on the ratio of the length of the areola to the length of the head portion of the cephalothorax, and on the presence or absence of lateral rostral spines. According to Creaser the eastern subspecies has an areola length half or less than half of the length of the head with lateral rostral spines present or absent, while the

western subspecies has an areola length of more than half the length of the head, with a complete absence of lateral rostral spines. Illinois, Michigan, Minnesota and possibly Indiana were suggested as a region of intergradation between the eastern and western subspecies.

An examination of the data indicated that perhaps the true situation was not a case of two freely intergrading subspecies, but rather a single species in which observable differences in populations were expressed in an east-west cline. From the data cited it also seemed that the differences in proportion of the areola length to head length might be dependent upon age or sex rather than upon geographic variation. Further, previous workers have considered the lateral rostral spines as extremely variable structures whose presence or absence is due to individual variation, and whose presence is more characteristic of young individuals than old individuals.

A random sample of *Orconectes immunis* was collected at approximately the same date on two consecutive years from a locality 2½ mi. SE Snow Hall, Kansas Univ., Lawrence, Douglas County, Kansas. An anlysis of the ratio of areola length to head length was made. No significant differences were found in this ratio in females in the two successive years, in males in the two successive years, nor between males and females of the two years combined. Using cephalothorax length as an index to age, no correlation was found between areola-head length ratio and age. The results of this analysis thus apparently confirm Creaser's contention that variations in areola-head length ratios are geographic variations and not age or sex variations.

According to Creaser (1933:15) ratios of areola length to length of the head varied in the following manner (selected sample of Creaser's data):

Locality	Ratio
Englewood, Colorado	1:1.70
Washington County, Kansas	1:1.85
Palo Alto County, Iowa	1:1.94
Carmi, Illinois	1:2.00
Reelfoot Lake, Tennessee	1:2.20
Cayuga County, New York	1:2.10
Lake Winnisquam, New Hampshire	1:2.23
Pittsfield, Massachusetts	1:2.02

The mean ratio of areola length to head length of all specimens from the samples collected near Lawrence, Douglas County, Kansas, is 1:1.99. Some of the individuals of *O. immunis* from certain Kansas localities show a slight development of lateral rostral spines,

although the lateral rostral spines are never sharply distinct. Further, the mean ratio for cephalothorax proportions of Douglas County specimens is only .01 mm. different from the material from Carmi [White County,] Illinois which seemingly would put the Douglas County individuals well within the range of intergradation of Creaser's eastern and western subspecies yet they are from what appears to be the area occupied by *O. immunis pedianus* alone. In fact the New Hampshire specimens and the Reelfoot Lake specimens appear to show greater discrepancies in this areola-head length ratio than individuals in any other part of the entire range of the species, suggesting that if any individuals are subspecifically distinct it must be these, which are on the periphery of the known territory occupied by the species. Further, specimens from Pittsfield, Massachusetts have proportions only .03 mm. different from Lawrence specimens.

In our opinion the data indicates that *Orconectes immunis* is a widely distributed species which shows east-west clinal variations in the areola-head length ratio and in the presence or absence of lateral rostral spines (especially in young individuals), but is a species which manifests local variations in both of these characteristics. We regard the geographic variations as not constant enough to warrant subspecific designations.

Cambarus diogenes diogenes Girard

Plate XCVII, Text fig. 8

Cambarus diogenes Girard, 1852, Proc. Acad. Nat. Sci. Philadelphia, vol. 6, p. 88.
Cambarus nebrascensis Girard, 1852, Proc. Acad. Nat. Sci. Philadelphia, vol. 6, p. 91.
Cambarus obesus Hagen, 1870, Illinois Cat. Mus. Comp. Zool., no. 3, p. 81.
Cambarus diogenes diogenes Hobbs, 1942, Amer. Midl. Nat., vol. 28, no. 2, p. 354.

Recognition Characters

Male form I: (Plate XCVII, fig. F) Rostrum subtriangular, without lateral spines, depressed, longer than broad; postorbital ridges decurved anteriorly, with or without small anterior tubercle; suborbital angle acute; cephalothorax robust, laterally compressed, punctate dorsally and posterolaterally, granulate anterolaterally; cephalic groove deeply cleft, continuous laterally, lateral spines absent; areola obliterated at least in middle; head length contained in cephalothorax length approximately 1.65 times; telson evenly rounded caudally, with paired lateral spines; antennae longer than cephalothorax, antennal scale (Plate XCVII, fig. G) roughly rec-

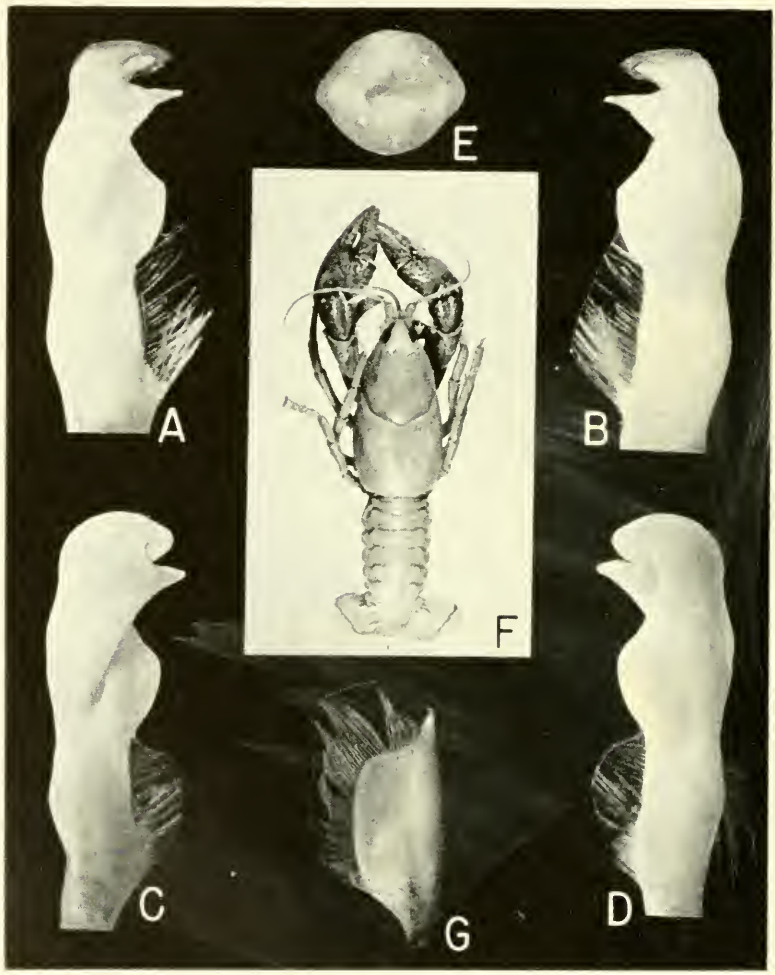

PLATE XCVII

Cambarus diogenes diogenes Girard

FIG. A, ♂ form I gonopod, medial view, × 5.
FIG. B, ♂ form I gonopod, lateral view, × 5.
FIG. C, ♂ form II gonopod, medial view, × 5.
FIG. D, ♂ form II gonopod, lateral ivew, × 5.
FIG. E, Annulus ventralis, × 5.
FIG. F, ♂ form I, × ½.
FIG. G, Antennal scale, × 5.

tangular in outline, lateral spine prominent; chelae heavy, punctate, with rows of deep punctations on fingers, movable finger and palm tuberculate medially, movable finger recurved, opposed edges of fingers with single row of rounded tubercles, largest tubercle in proximal half of row on immovable finger; carpus with one distinct and several indistinct spines medially, and one moderately produced ventral spine; anterior process of epistoma subtriangular, margin smooth; ischius of third pereiopods with strongly pointed hooks.

Gonopods (Plate XCVII, fig. A, B) stout, terminating in two short processes bent at approximately 90° to axis of shaft, lateral process (central projection) corneous, thin, bladelike, medial process with "awl-like" tip; tips of gonopods reaching base of third pereiopods with abdomen flexed.

Male form II: Chelae proportionately less robust than male form I; hooks on ischius of third pereiopods with rounded apex; processes of gonopods (Plate XCVII, fig. C, D) thick, noncorneous, with tips closely apposed, medial process with "awl-like" point.

Female: Chelae proportionately less robust than male form I; annulus ventralis (Plate XCVII, fig. E) roughly quadrangular in outline, deepest portion of sinus displaced either to right or left of midsagittal plane, sculpture variable.

Ecological Notes

A summary of the known ecology of *Cambarus diogenes diogenes* up to 1903 is given in Harris (1903:85), but in view of more recent work a new summary seems advisable at this time.

Girard (1852:89) first described *C. d. diogenes* as a burrowing species, and the burrows of *C. d. diogenes* have since been described by many other authors. Girard reported the burrows as circular at the ground surface varying in diameter from 7/10 to 1½ inches, surrounded by a chimney. He described the subsurface ramifications of the burrows as being simple or complex. A simple burrow was described as sloping gently and more or less tortuously from the surface opening for a distance of 5 to 10 inches after which it became vertical for 6 or 8 inches terminating in a "bottle shaped enlargement." The complex burrows were recorded as having several openings with inclined channels converging toward the top of the vertical channel. The burrows were observed to be partially full of water in March and April with the bottom enlargement full of soft mud. Other burrows were described as obliquely inclined throughout, composed of a series of chambers, with a deep tubular

vertical channel extending downward from one of these chambers. Bundy (1882:183) traced a *Cambarus obesus* (= *C. d. diogenes*) burrow for 12 feet without reaching the end of the burrow. Tar (1884:127) recorded burrows of *C. d. diogenes* as increasing in depth with increasing distance from a stream bed. He also observed that the size of the chimney at the mouth of the burrow varied directly with the size of the burrow. In deeper burrows he found enlargements which he considered as previous terminations of the burrow at previously higher water table levels. Engle (1926:96) reported a shallow burrow in disintegrated limestone on the bank of a creek. Subsequent workers have confirmed the observations of the workers cited above.

The chimneys which are sometimes characteristic of the burrows of this species were thought by Abbott (1884:1157) to be designed by the crayfish, but other workers, Tarr (1884:127), Schufeldt (1896:89), Ortmann (1906:421), and Engle (1926:96) concurred that the chimneys of this crayfish are not designed but are simply the result of disposal of materials excavated from the burrow. Schufeldt (1896:86) recorded chimneys as varying in height from that of a low mound to structures as much as a foot in height. Ortmann (1906:421) observed that the form of the pile built up depends solely on terrain, angle of the burrow at the mouth and on the consistency of the soil. In fact he observed that few *C. d. diogenes* burrows have any chimney at all. Hobbs (1942:166) observed that in burrows which have many openings there may or may not be a chimney surrounding each opening. Williams' observations confirm this statement.

Burrow openings are sometimes sealed over. Girard (1852:87) concluded that sealing was accomplished by bringing up pellets of mud which were allowed to rest on the edge of the chimney and were subsequently withdrawn to close the aperture. Abbott (1884:1157) considered the sealing as due to accidental "cave ins" of the chimney while Schufeldt (1896:88) suggested that the burrow plug might be fashioned by the crayfish by backing up the burrow and packing mud over the burrow opening with the abdomen, telson and uropods. Ortmann (1906:422) thought that the burrow plug was constructed by the crayfish. We have observed what appeared to be marks of the chelae on the underside of burrow mouth plugs. The method of sealing is unknown.

Ortmann (1906:420) described the method of burrowing. According to him the crayfish pushes the pincers into the mud, then pulls them toward the ventral side of the body thus pressing a lump

of mud against the antero-ventral aspect of the body. The piece of mud is thus carried to the mouth of the burrow and dropped.

The consensus of many workers indicates that *C. d. diogenes* is primarily a burrower along the banks of streams or in marshy places. We have found the species in burrows along stream banks, in a marshy area fed by an artesian well, in a muddy burrow by a spring-fed pool, and have seined one specimen from a farm pond.

Bundy (1877:171) recorded a *Cambarus obesus* (= *C. d. diogenes*) female in berry caught on New Year's Day, 1876. Hargitt (1890:114) found mating pairs of *C. d. diogenes* in March, April and May and on two occasions found females in berry in midsum-

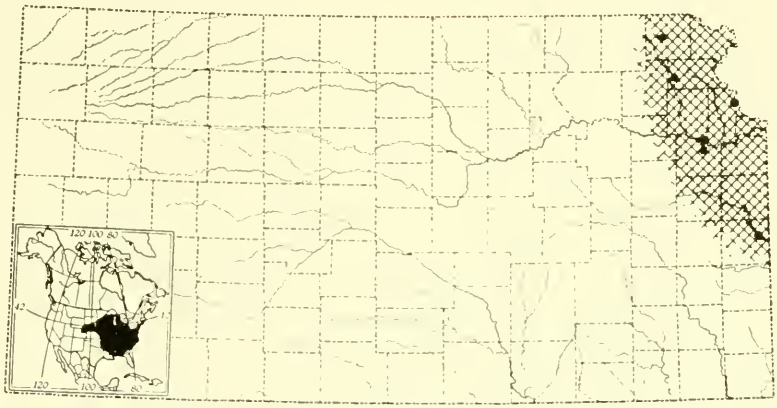

FIG. 8. *Cambarus diogenes diogenes*, records in Kansas. Inset shows distribution in North America. Open circle = record from literature.

mer. Hay (1896:491) recorded spring as the breeding season and found pairs in copulation on April 2, 1892. Eggs in this case were laid from April 18-30. Creaser and Ortenburger (1933:41) reported a female with young taken in Michigan in June. There are female *C. d. diogenes* in berry in the Kansas University collection which were collected near Muscotah, Atchison County, on 11 April, 1947. Williams observed *C. d. diogenes* in copulation on 12 October, 1947. Specimens taken near Muscotah, Atchison County, were brought to Lawrence alive and placed in a galvanized washtub in water approximately 1 inch deep at 4:30 PM. (The specimens had been collected between about 11:00 AM and 3:00 PM that day). At 6:00 PM a pair was observed in copulation. Copulation lasted for approximately 40 minutes, and the procedure agreed with the description given by Andrews (1895:867; 1904:167).

RECORDS IN KANSAS

Atchison County: Lot 152. 1½ mi. S Muscotah (E ½, sec. 16, T. 6 S, R. 17 E); *Brown County:* Lot 157. 7/10 mi. E Fairview (NE ¼, SE ¼, sec. 26, T. 2 S, R. 16 E); *Douglas County:* Lot 75. 2 mi. S, ¾ mi. E Snow Hall, Kansas Univ., Lawrence (NE ¼, NE ¼, sec. 18, T. 13 S, R. 20 E); Lot 749. 4 mi. N, 3 mi. E Snow Hall, Kansas Univ., Lawrence (sec. 16, T. 12 S, R. 20 E); *Leavenworth County:* Leavenworth; *Linn County:* Lot 756. Roadside ditch 1 mi. S Trading Post.

KNOWN RANGE

Alabama, Arkansas, Colorado, Delaware, District of Columbia, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Michigan, Minnesota, Mississippi, Missouri, Nebraska, New Jersey, North Carolina, Ohio, Oklahoma, Pennsylvania, Tennessee, Virginia, West Virginia, Wisconsin, and Wyoming.

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Mollusca on the University of Kansas Natural History Reservation

BY

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ABSTRACT: The University of Kansas Natural History Reservation consists of approximately 1 square mile of wooded, hilly land situated on the north slope of the Kansas River Valley in Douglas County, Kansas. Until 1948 the land was subjected to cultivation and grazing. The mollusean fauna was studied soon after agricultural activities ceased on the Reservation. Four species of aquatic mollusks and 21 species of terrestrial gastropods were observed at 10 stations, which were selected for their differenees in local habitat conditions. All species are illustrated by photographs, and the distribution of mollusks at the several collecting stations is shown by a tabular compilation of the fauna. Photographs of the collecting stations are included.

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INTRODUCTION

The principal aim of this report is to record the kinds of mollusks that live on the University of Kansas Natural History Reservation. This report is the first in what is expected to be a series covering the various invertebrate and vertebrate groups to be found on the Reservation.

In the years preceding this study much of the land now in the University of Kansas Natural History Reservation was grazed by domestic livestock while other parts were cultivated. The ground is now being allowed to revert to natural conditions. The information here recorded should be useful in discovering changes in the molluscan population which may result from changes in the flora and the remainder of the fauna.

The Reservation is on or near the southern and western margins of the range of many northern and eastern species as well as on or near the northern margin of the ranges of a few snails of southern distribution.

LITERATURE

Literature directly concerned with the ecology of land and freshwater snails is scarce and only within the last two decades have papers appeared in any appreciable quantity. One of the earliest studies was a quantitative account of the molluscan fauna of one log (Van Hyning, 1904:130). Sterki (1911:98) noted the effect of civilization on several species of terrestrial snails, and this subject has received further treatment from Archer (1937:117) and Goodrich (1940:6) who studied the effects of civilization on aquatic

Mollusca. Archer (1935:77;1939:1;1941:4) has published accounts of the ecology of faunas of snails in North Carolina, Michigan, and Alabama. The effects of environmental conditions upon characters of the shell have been discussed by Goodrich (1939:124).

Literature concerning the molluscan fauna of Kansas has been reviewed thoroughly by Franzen and Leonard (1947:314) in their monographic treatment of the Pupillidae of Kansas.

History and Description of the Area

The University of Kansas Natural History Reservation is situated four miles north and one and one-half miles east of the Kansas River bridge at Lawrence, Kansas. It includes all of section 4, T. 12S, R. 20E, Douglas County, Kansas, with the exception of fifty acres in the southwest corner.

This section lies among the hills which flank the north border of the Kansas River valley. The character of these hillsides is much the same throughout the lower region of the Kansas River, being sparsely to heavily wooded. Although erosion has been slow, owing to the cover of trees and grass, it has been sufficient to produce irregular topography along the sides of the valley. The valley terraces extend in fingerlike fashion into numerous small valleys which dissect the hills. Between the hillsides, left in the wake of eroding gully streams, there are small fields and meadows sloping gently toward the valley floor. On the hilltops, the extensions of the drier upland area are comparatively level and are either cultivated or, more often, used for grazing. The residual soil is permeated with small limestone rocks and each hillside is crowned with outcropping limestone. In the east central part of the Reservation a small stream exposes a thick bed of shale.

The land now utilized as the University of Kansas Reservation was willed to the University of Kansas by the late Governor Charles Robinson (1818-1894). Upon the death of the widow of Governor Robinson in 1914 the lands came under the active management of the University and on July 1, 1948, Dr. Henry S. Fitch and associates began a study of the biota of the area.

Within the memory of older local residents the land has undergone little change and until late in 1948 most of the untimbered areas were either cultivated or subject to grazing. Grazing had been discontinued on most of the timbered areas some time prior to 1938. In 1936, under the CCC program, some of the land was cleared and a series of check dams were constructed in the grazed meadow (Plate XCVIII) in an attempt to halt the severe erosion

of that pasture. The present policy of the administration is to allow the Reservation to revert to natural conditions.

The first accounts by early settlers describe this section of Kansas as having few trees except along waterways, the slopes and valleys being covered by grass. In this area big bluestem grass, which is resistant to the spread of trees, was abundant. The settlers planted trees and destroyed most of the big bluestem by turning the sod or by overgrazing. As a result, the wooded areas were extended and by the late 1800's the terrain was much as it is today.

CLIMATE

The climate of Kansas is characterized by extremes of temperature and precipitation. "The State lies across the path of alternate masses of warm moist air moving north from the Gulf of Mexico and currents of cold, comparatively dry, air moving from the polar regions. Consequently, its weather is subject to frequent and often sharp changes, usually of short duration" (Flora, 1948:1).

The higher temperatures and lessened rainfall of the summer months often result in a hot, dry period. For example, in 1936 Lawrence recorded an average monthly rainfall of .84 inch for the three summer months and an average temperature of 88 degrees, with a high of 113 degrees for the month of July (Flora, 1948:70, 192). In other years the summer months have passed with temperatures no higher than 100 degrees and with an average monthly rainfall of more than five inches. Annual precipitation is especially subject to year to year variation. Douglas County records show 42.93 inches annual rainfall in 1935 and the following year, the driest in the state's history, only 22.12 inches (Flora, 1948:70).

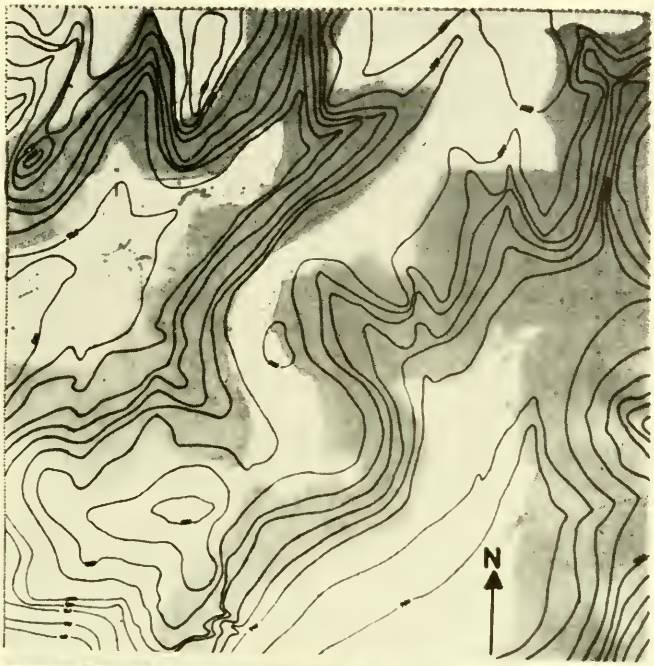
The prevailing wind in the northeastern section of the state is from the south during all the months except January, February, and March when it is from the north or northwest. This prevailing south wind has a drying effect on the soil which is particularly noticeable when one compares the south-facing hillsides with the protected and hence, more moist, north-facing slopes. This condition is reflected in the flora of the two slopes as well as in the molluscan fauna found there. On the north-facing slopes are found

PLATE XCVIII

Upper figure: Contour map of University of Kansas Natural History Reservation. Contours are drawn at intervals of 20 feet. Elevation ranges from 900 to 1060 feet above sea level.

Lower figure: Aerial photograph of the Reservation. Letters indicate the position of each of the 8 collection stations discussed in the text.

PLATE XCVIII



such trees as shagbark hickory (*Carya ovata*), black oak (*Quercus velutina*), white ash (*Fraxinus americana*), and black walnut (*Juglans nigra*) while on the south facing slopes elm (*Ulmus americana*), honey locust (*Gleditsia tricanthos*), osage orange (*Maclura pomifera*), and yellow oak (*Quercus muehlenbergii*) predominate.

The effect of such climatic conditions upon the molluscan fauna is, of course, pronounced. Aquatic molluscan life is limited, in many instances, to those species which can exist in ponds, lakes, and streams of a more or less ephemeral nature. Terrestrial snails are limited to those species that can survive the frequent hot, dry periods either by making physiological adaptations, that is to say, by aestivation and the formation of an epiphragm, or by limiting their habitats to the most moist situations. While climatic conditions do not permit as many species to occur here as are found in more northern and eastern states, the individual snails of local species are often found in abundance.

METHODS

From September 20 to October 1 of 1948 first hand inspection was made of the Reservation in order to select collecting stations. Collecting by Goble was initiated on October 1, 1948, and continued until mid-November when winter weather halted further field work. From March 1, 1949, to June 20, 1949, regular field trips were made to the Reservation. In this period field notes were taken on the flora of each station and snails were collected and given a field number which designated both the station and the date of collection.

The specimens were collected in vials and taken to the laboratory. The snails were then cleaned and placed in a cabinet where they were available for future reference and study. If it was found necessary to kill the live snails and remove the soft parts; they were killed by placing them in boiling water for several minutes. The bodies were then easily removed with a small needle. It was not necessary to remove the soft parts from snails as small as pupillids. If the soft parts were to be preserved, the snail was drowned in water that had been heated to remove the oxygen. When this was done the animal died in an extended position.

Field equipment included an aspirator, which was most useful in the collection of small shells; vials with cotton plugs; screens for sifting soil and stream gravel; a 10x hand lens; a one-foot quadrat frame for population studies; and a folding rule.

After the specimens had been studied and all the data assembled

catalogue numbers were assigned and the collection was filed in the Mollusk Collections of the University of Kansas Museum of Natural History.

In the following account no attempt has been made to list the complete flora of the various collecting stations. The predominant flora is listed in order to convey to the reader a picture of the habitat conditions.

For the sake of brevity, stations are referred to by the letter S followed by a letter indicating a particular station.

COLLECTING STATIONS

Station A—Small Stream

This stream arises in the extreme northeast corner of the section and flows to the south. It drains that part of the Reservation to the southeast of the high plateau that divides the section diagonally into two approximately equal halves. One mile south of the Reservation it empties into a small stream known locally as Mud Creek. Collecting was limited to that part of the stream within 800 feet of the southern boundary of the Reservation, this area having an abundance of plant cover not to be found along the more northern parts of the stream.

Except for periods following rains the stream is less than five feet in width, receiving a constant water supply from small seeping springs along its course. The larger pools are only six to ten inches in depth. The banks are high and steep, in many places being nearly vertical. In the southern half of the Reservation the stream bed is entrenched approximately fifteen feet below the level of the surrounding fields. Crayfish (*Orconectes nais*) are numerous and the larger pools support schools of small fish. The absence of the larger species of fish eliminates the possibility of a unionid mussel fauna.

Living aquatic snails were represented by a large colony of *Physa hawni* Lea. These snails were collected from the margin of the stream where they were crawling on leaves, roots, debris, and plants which were growing in the water. A few dead specimens of *Pisidium* cf. *compressum* Prime were recovered from gravel.

Station B—Silted Pond

This small pond is located at the eastern end of the meadow (Pl. XCVIII) where the pond receives drainage from the hills which border it on three sides. The pond was formed by the construction of an earthen dam more than twenty years prior to this

study. In the ensuing years the pond has gradually filled with silt until, at the time this study was made, it was no more than two feet deep when filled and remained dry many weeks during the year in the absence of rains.

During the wet seasons several species of aquatic plants are abundant in the pond. Cattail (*Typha latifolia*) and bulrush (*Scirpus sp*?) occur around the margins of the pool as do willow (*Salix sp*?) and cottonwood seedlings (*Populus deltoides*). Sweet clover (*Melilotus alba*), ragweed (*Ambrosia trifida*), and dock (*Rumex altissimus*) are found along the banks. Near the pond at the margin of the wooded area are such trees as yellow oak (*Quercus muehlenbergii*), shagbark hickory (*Carya ovata*), poplar (*Populus alba*), and ash (*Fraxinus americana*).

The snails found here were *Helisoma trivolvis, Physa hawni, Sphaerium sp,* and *Succinea concordialis* which is a terrestrial snail found close to water. They are species which can survive long dry periods. Specimens were first collected during a dry period lasting from mid-September to late December of 1948. No living snails were found and a re-check of the pond during the wet season failed to reveal any living examples. A search for aestivating individuals in the summer also proved fruitless.

STATION C—BANKS OF SMALL STREAM

The location and a description of the small stream is to be found under the discussion of station A; the collections were made on that portion of the stream within 800 feet of the southern boundary of the Reservation.

Along this part of the stream the slope of the bank varies from 20 to 80 degrees. The steepness of the banks and the narrowness of the stream affords protection from both the sun and wind, causing the relative humidity to be high. The soil is loose and moist and lacks a heavy cover of decaying leaves, although the underbrush is dense.

There are fewer kinds of trees at this station than on the higher slopes. The few large trees are elm and cottonwood. The underbrush is largely seedlings and young trees of the same species. In the underbrush coralberry, smooth sumac, prairie mimosa, and wild grape are present. Near the water, bulrush and scouring rush grow in large patches.

This station is the most moist of the truly terrestrial habitats, and *Vertigo ovata* and *Lymnaea parva* were found only at this station.

Station D—Decaying Log Habitat

In the interest of wild life conservation, logs on the Reserve proper are left undisturbed but a number of logs were examined at a place in the southwest corner of the section. This particular place was near the summit of the north facing slope immediately below the limestone outcrop which caps all the hills in this area. The logs were in the oak-hickory-walnut association of station E.

Thirteen species of snails were recovered from decaying logs. Although the collecting was not so remunerative as on the forest floor, the percentage of living snails was much higher. Only four species occurred in abundance. These were *Zonitoides arboreus*, *Retinella electrina*, *Stenotrema monodon aliciae*, and *Strobilops labyrinthica*. Each of these species is limited to woodland areas on the Reservation. *Zonitoides arboreus*, in particular, is closely associated with decaying logs. The examination of a single log, eight feet long and twelve inches in diameter, revealed twenty-six living snails of this species.

Station E—North-facing Wooded Slope

This slope is situated south of the meadow. Two rectangular fields separate the grazed part of the meadow (SI) from the wooded slope (Pl. XCIX). Collecting on this hillside was restricted to an area within 1350 feet of the western boundary of the Reservation.

The slope is gentle, averaging a one and one-half inch drop per linear foot. The loose, rich soil is covered by a thick layer of moist humus. Outcropping limestone rocks dot the hillside and small flat stones are scattered throughout the soil. Rocks, decaying logs, and bases of trees are covered with moss.

On the upper half of the hillside yellow oak, shagbark hickory, and black walnut make up the bulk of the trees while farther down the slope black oak and elm predominate with honey locust and osage orange occurring at the margin of the wooded areas. Redbud and coralberry are the most abundant shrubs in the understory although patches of smooth sumac and wild plum are also common. Bittersweet (*Celastrus scandens*), wild grape, greenbrier (*Smilax hispida*), and wild rose (*Rosa sp.*) are scattered over the hillside. Virginia creeper (*Parthenocissus quinquefolia*) predominates in the lower vegetation. The abundance of redbud is the distinguishing feature of the flora of this slope.

There are eighteen to twenty-five snails per square foot in the

yellow oak-hickory-walnut area as against an average of fewer than five individuals in the more poorly drained area farther down the slope. It is worth noting that snails occur far less frequently on this slope than on the south and west facing hillsides (SF and SG) where they average from thirty to fifty specimens per square foot.

STATION F—WEST-FACING SLOPE

This steep slope is situated north of the meadow and immediately west of an old quarry (Pl. XCIX). Collecting was limited to the west face of the hill.

While the soil and general appearance of the slope is similar to the south facing slope (SG) the greater steepness (five inch rise per foot) and protection from the early morning sun is reflected in the flora and molluscan fauna found there. In many places all humus has been washed off the hillside. On other parts of the slope the humus is light except around the bases of trees and shrubs. In general this station is more moist than the south facing slope, being somewhat protected from the prevailing winds as well as from the direct rays of the sun. However moisture is less abundant than on the north facing hillsides.

On this west-facing hillside the large trees are limited to a few scattered honey locust and elm. Small trees are numerous and the underbrush is dense. Yellow oak is by far the most common tree and on this slope it grows to a height of only ten to fifteen feet. Also scattered over the hillside are osage orange, hackberry (*Celtis occidentalis*), crabapple (*Malus angustifolia*), and redbud. Coralberry and gooseberry (*Ribes missouriense*) are abundant in the underbrush and poison ivy (*Rhu toxicodendren*) and Virginia creeper are the dominant species of the low vegetation.

PLATE XCIX

FIG. A. Silted pond habitat, Station B. Photograph made when there was no open water (November, 1950), in the pond.

FIG. B. Wooded, north-facing slope in distance, Station E.

FIG. C. Wooded, west-facing slope, Station F.

FIG. D. Grazed meadow, Station I, and wooded, south-facing slope in distance. Grasses and herbs have flourished in the meadow since cattle were withdrawn. Photograph made in November, 1950, 2 years after grazing of the meadow ceased.

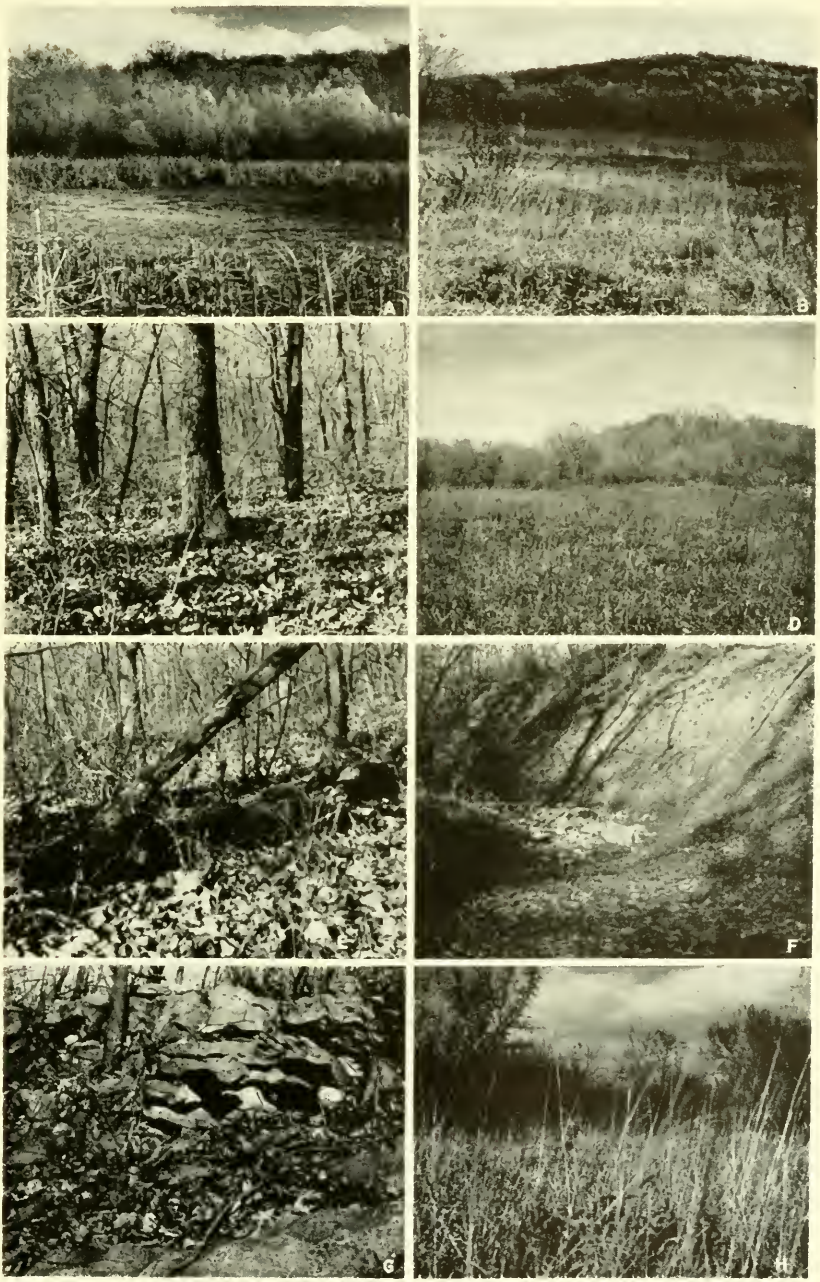
FIG. E. Fallen log habitat, Station D.

FIG. F. Small stream, Station A, and banks of stream, Station C. Stream had no open water when photograph was made, (November, 1950).

FIG. G. Limestone ledge, which is found near the summit of the hills, (Station J).

FIG. H. Ungrazed meadow (Station H) with luxuriant growth of bluestem grass and herbs.

PLATE XCIX



The snail fauna at this station is unusual in that *Succinea avara,* a moisture loving species, and *Pupoides albilabris,* a snail of more arid habitats, occur on the same hillside. They do not occur together, however, for *P. albilabris* is found only on the steepest areas in the lower half of the hillside, whereas S. *avara* occurs near the top of the slope among the outcropping limestone ledges. Another peculiarity of this snail fauna is the abundance of *Gastrocopta holzingeri* which in many places on the slope is the most common species. It is not one of the common snails of Kansas and its occurrence in such numbers is indeed surprising. The dead and living specimens from this station average thirty to thirty-five per square foot.

STATION G—SOUTH-FACING WOODED SLOPE

This hillside lies to the north of the meadow and directly opposite Station E. The collecting area included only that part of the slope within 675 feet of the west boundary of the Reserve.

This south-facing slope is steeper than the north-facing hillside, averaging a two and two-thirds inch rise per foot. The rocky soil resembles that of the other hillsides but is not so moist nor so rich in decomposed vegetation as the north-facing hills.

The American elm and honey locust are the most abundant trees at this station. The honey locust is particularly numerous along the margin of the wooded area and in the open spaces farther up the hillside. Other scattered trees include Osage orange, yellow oak, crabapple, and hackberry. The underbrush is composed chiefly of coralberry, smooth sumac, and the seedlings of elm and honey locust. Wild plum, aromatic sumac (*Rhus aromatica*), gooseberry, blackberry (*Rubus ostryifolius*) and wild grape are also present. Conspicuous by its absence is the redbud.

From the standpoint of the number of specimens of snails present, this station is first; it has an average of forty-six dead and living snails per square foot. This figure includes only shells found on the surface and in the loose soil to a depth of one inch. As far as number of species is concerned the slope was fifth among the eight terrestrial stations. Only eleven species were collected from this station as compared with fourteen from the north-facing slope (SE) and thirteen from Station C and the same number from Station D. Three species, *Gastrocopta armifera, Vallonia parvula,* and *Retinella indentata,* comprised eighty percent of the snail fauna.

Station H—Ungrazed Grassland

This small plot of high grass and herbs is in the extreme northwest corner of the Reservation on the edge of the plateau (Pl. XCVIII), and slopes gently to the east, draining into a gully that lies between the grassland and the north-south county road. The area is well covered by big bluestem grass (*Andropogon furcatus*). Prairie mimosa and compass plants (*Silphium laciniatum*) are scattered throughout the grass.

This habitat is less favorable for most of the species of snails than other habitats; less than one half of the species of snails found on the Reservation occur here. Moreover, an unusually large percentage of the specimens collected were empty shells. *Gastrocopta armifera* was the most common species but even it was not abundant.

Station I—Grazed Meadow

The meadow extends in a northeasterly direction from an area near the mid-point of the west boundary of the Reservation to the north-central part of the section (Pl. XCVIII).

This station was grazed until March, 1949, when the cattle were removed from the Reservation. Even in this short period the grasses have recovered in great measure and erosion which was progressing at an alarming rate probably will be less rapid. The soil is well packed and becomes dry during periods without moisture, but with the improvement in grass and weed cover the soil will become looser and more moist.

The flora consists of mixed weeds and grasses. The predominant species are listed below:

Panicum dichotomiflorum—Fall panicum
Setaria lutescens—Yellow foxtail
Bromus inermis—Smooth brome
Bromus purgans—Canada brome
Capsella bursapastoris—Shepherd's purse
Erigeron philadelphicus—Fleabane
Lepidium sp?—Peppergrass
Ceanothus americanus—New Jersey tea
Desmanthus illinoensis—Prairie mimosa
Asclepias tuberosa—Butterfly weed

At the time the collection was made snails were all but completely absent from the meadow. *Gastrocopta armifera* was found at the margin of the meadow under small rocks but none was obtained from farther than thirty feet from the timbered areas. A

single dead specimen of *Gastrocopta procera* was found near the center of the meadow under cow dung in an area covered by buffalo grass. In an ungrazed part of the meadow near the pond there was a large colony of *Bulimulus dealbatus*.

STATION J—ARID LIMESTONE HABITAT

All the hills on the Reservation are capped by limestone which outcrops at the brow of each hill. Coinciding with the margin of the timbered areas, these rocky ledges are exposed to both the sun and the wind.

Collecting was not limited to any particular section of the Reservation, the habitat being similar at the summits of the various hillsides.

The flora of such habitats consists chiefly of coralberry, smooth sumac, elm, and honey locust. Gooseberry, wild rose, and stunted specimens of yellow oak and other species are common.

CHECK LIST OF MOLLUSCAN FAUNA

Phylum Mollusca
- Class Gastropoda
  - Order Pulmonata
    - Suborder Basommatophora
      - Family Physidae
        - Genus *Physa* Draparnaud
          - *Physa hawni* Lea
      - Family Planorbidae
        - Genus *Helisoma* Swainson
          - *Helisoma trivolvis lentum* (Say)
      - Family Lymnaeidae
        - Genus *Lymnaea* Lamarck
          - *Lymnaea parva* Lea
    - Suborder Stylommatophora
      - Family Pupillidae
        - Genus *Gastrocopta* Wollaston
          - *Gastrocopta armifera* (Say)
          - *Gastrocopta contracta* (Say)
          - *Gastrocopta holzingeri* (Sterki)
          - *Gastrocopta pentodon* (Say)
          - *Gastrocopta procera* (Gould)
        - Genus *Vertigo* Draparnaud
          - *Vertigo ovata* Say
        - Genus *Pupoides* Pfeiffer
          - *Pupoides albilabris* (C. B. Adams)
      - Family Succineidae
        - Genus *Succinea* Draparnaud
          - *Succinea avara* Say
          - *Succinea concordialis* Gould

Family Vallonidae
Genus *Vallonia* Risso
Vallonia parvula Sterki
Family Strobilopsidae
Genus *Strobilops* Pilsbry
Strobilops labyrinthica (Say)
Family Endodontidae
Genus *Helicodiscus* Morse
Helicodiscus parallelus (Say)
Family Polygyridae
Genus *Stenotrema* Rafinesque
Stenotrema monodon aliciae (Pilsbry)
Family Bulimulidae
Genus *Bulimulus* Leach
Bulimulus dealbatus (Say)
Family Limacidae
Genus *Deroceras* Rafinesque
Deroceras laeve (Müller)
Family Zonitidae
Genus *Hawaiia* Gude
Hawaiia minuscula (Binney)
Genus *Retinella* (Shuttleworth) Fisher
Retinella electrina (Gould)
Retinella indentata (Say)
Genus *Zonitoides* Lehman
Zonitoides arboreus (Say)
Genus *Euconulus* Reinhardt
Euconulus chersinus cf. *polygyratus* (Pilsbry)
Class Pelecypoda
Order Eulamellibranchiata
Family Corbiculidae
Genus *Sphaerium* Scopoli
Sphaerium sp?
Genus *Pisidium* Pfeiffer
Pisidium cf. *compressum* Prime

ACCOUNTS OF SPECIES

Physa hawni Lea

Plate C, fig. 2

Physa hawni Lea, 1864, Proc. Acad. Nat. Sci. Philadelphia, p. 114; Baker, 1928, Wisconsin Geol. and Nat. Hist. Survey, Bull. 70, pt. 1, p. 453.

Recognition characters: Shell sinistral, imperforate, light brown; size variable, approximately 13 mm. in height; whorls 5; spire sharply conic; body whorl large, ¾ or more of length of shell; aperature elongate, oval; lip thin with a distinct parietal callus.

Type locality: Verdigris River, Kansas.

Geographic distribution: Texas, northward in Oklahoma, Arkansas, Missouri, and Kansas.

Ecology: This hardy species lives in bodies of freshwater of all sizes, whether they be temporary or permanent, and whether natural or artificial. Franzen and Leonard (1943:408) state that in northeastern Kansas *P. hawni* is "Common in roadside pools in colonies of considerable size. Much less common than *P. anatina* in streams, although Lea described it from the Verdigris River, Kansas." Alice Leonard (1943:238) reports *P. hawni* as "thriving in stock tanks supplied from wells," where there were no natural bodies of water within a distance of several miles.

P. hawni occurs on the Reservation at stations A and B. Ecological conditions at station B are described in the above account of *Helisoma trivolvis.* All the specimens from the pond (SB) were small and immature. A colony that included mature snails was found at the small stream (SA), where the snails were abundant among the plants and debris along the banks.

Helisoma trivolvis lentum (Say)

Plate C, fig. 9

Planorbis trivolvis Say, 1817, Nicholson's Encyc., 1st. American Ed., vol. 2, (no pagination), pl. 2, fig. 2.
Helisoma trivolvis, Baker, 1928, Wisconsin Geol. Nat. Hist. Survey, Bull. 70, pt. 1, pp. 330-334, pl. 20, figs. 1-13, 22, 23.

Recognition characters: Shell discoidal, flat, sinistral; color yellowish brown; whorls 4, whorls of spire form slightly concave surface; lip of aperature sharp, with thin parietal callus; surface sculptured with fine, oblique lines.

Type locality: "French Creek, near Lake Erie" (Baker, 1928:331).

Geographic distribution: "Atlantic coast and Mississippi River drainages, northward to Arctic British America and Alaska and southward to Tennessee and Missouri. The southern distribution is not clear owing to mixing with related species" (Baker, 1928:332). *H. trivolvis* is widely distributed in Kansas.

Ecology: Helisoma trivolvis occurs in ponds and lakes throughout the state of Kansas. It is frequently found in ephemeral roadside pools. "It can survive long periods of drouth, apparently by burrowing into the mud in the bottom of drying pools" (A. Leonard, 1943:235).

H. trivolvis and other aquatic species were collected from the pond (SB) on October 8 and October 27, 1948. At that time the pond was dry and had been since mid-September. No living examples were found on those dates, although from the color of the shells and their number, it was obvious that the pond had recently

supported a flourishing population. The pond became filled with water in early December, 1948, but at the time of this study no living snails were observed in the pond.

Lymnaea parva (Lea)

Plate C, fig. 8a

Lymnaea parva Lea, 1841, Proc. American Philosophical Soc., 2:33; Baker, 1911, Special Publ. No. 3, Chicago Acad. Sci., p. 243, pl. 29, figs. 5-14, Pl. 30, figs. 9-12; Franzen and Leonard, 1943, Univ. Kansas Sci. Bull., vol. 29, pt. 2, No. 9, p. 406, Pl. 30, fig. 6.

Recognition characters: Shell small, turreted, light brown; height variable; whorls 5; dextral; suture deeply impressed; body whorl inflated; aperature oval, about ⅓ height of shell; spire acutely pyramidal; outer lip thin; inner lip reflected, reducing umbilicus to a fissure; growth lines fine, irregular.

Type locality: Cincinnati, Ohio.

Geographic distribution: "Connecticut west to Idaho; James Bay and Montana south to Maryland, Kentucky, Oklahoma, southern New Mexico and Arizona" (Baker, 1911:32).

Ecology: Lymnaea parva is a typical inhabitant of very moist situations. Archer (1939:16) reports this snail, in Michigan, "on mud and decaying vegetation out of the water along the edges of pasture pools." Baker (1911:247), in reference to its aquatic life, states, "The animal is more prone to leave the water than any other of the Lymnaeas." In Kansas, *L. parva* is usually found in habitats similar to those described by Archer. Moist drift and other decaying vegetation provide an optimum environment.

Only a few dead specimens of *Lymnaea parva* were found on the Reservation. These were collected from the loose moist soil on the banks of the small stream (SA).

Gastrocopta armifera (Say)

Plate CI, fig. 23

Pupa armifera Say, 1821, Jour. Acad. Nat. Sci. Philadelphia, 2:162.
Gastrocopta ramifera, Pilsbry, 1948, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(2):874-877, fig. 472.

Recognition characters: Largest of the genus as represented in Kansas; oval; rimate; whorls 4½ to 6½; a large, bifed, angulo-parietal lamella; may have two palatal folds; basal fold; large, triangular, columellar lamella.

Variation in characters of the shell is the rule with this species. The height varies from 3.5 mm. to 5 mm. Other variable features are number of palatal folds, size of the basal fold, and size and shape

of the columellar lamella. These variations frequently occur among the individuals of a single population.

Type locality: Pilsbry (1948:875) has selected Germantown, Philadelphia, Pennsylvania as the type locality.

Geographic distribution: "It inhabits almost the whole country east of the continental divide, but is lacking in southwestern New Mexico, southern Texas, southern Florida, and the higher parts of the Alleghany Mountain system" (Pilsbry, 1948:875). This species is common throughout Kansas.

Ecology: In eastern Kansas *G. armifera* occurs in a wide variety of habitats. It may be found under leaf mold on wooded slopes, under limestone rocks on barren hillsides, beneath decaying wood, and among roots of tall grass. In other areas this snail does not enjoy such an ubiquitous distribution. In a paper concerning the Mollusca of Michigan, Archer (1939:23) reports, "This snail is very abundant in open country on slopes and in valleys but tends to avoid summit areas. It has not been found in woodland cover." In 1937 Archer wrote of *G. armifera* in Ohio, "*G. armifera* and *P. marginatus* (*P. albilabris*) are rare or absent in woods, but abundant in fields, on railroad embankments, and also in rocky, open country." Alice Leonard (1934:238) found that *G. armifera abbreviata* had "a distinct preference for woodlands . . ." in western Kansas. These inconsistencies in habitat occupied probably are related to differences in local climatic conditions.

On the University of Kansas Natural History Reservation *G. armifera* was collected from every terrestrial station, and was by far the most abundant snail. *G. armifera* is frequently associated with two other species, *Vallonia parvula* and *Retinella indentata.* At Station G, where eleven species of land snails are represented, these three species constitute 80 per cent of the total molluscan population. In some areas at this station the empty shells and living animals of *G. armifera* average eight per square foot. The species was found in greatest numbers at Stations F and G, where it occurs with surprising frequency under small limestone rocks in arid situations. On one rocky slope shells of *G. armifera* averaged seven specimens per stone, the stones ranging from four to eight inches in diameter. Several specimens were collected from under stones at the margins of the grazed meadow (S1) and from a similar environment on the plateau near the north boundary of the Reservation. *G. armifera* was also found under decaying logs beneath

humus on the north-facing slope but it was not common at either of these stations.

Gastrocopta contracta (Say)

Plate CI, fig. 11

Pupa contracta Say, 1822, Jour. Acad. Nat. Sci. Philadelphia, 2:374.
Gastrocopta contracta, Pilsbry, 1948, Acad. Nat. Sci. Philadelphia Monographs No. 3, 2(2): 880-881, fig. 474.

Recognition characters: Shell medium size for genus; ovate-conic; height 2.1 mm. to 3.0 mm.; rimate; whorls 4½ to 6; body whorl contracted just behind aperature; aperature trianguloid, apex forming base of aperature; aperature almost closed by folds and lamellae; large fused angulo-parietal; two palatal folds connected by a callus; columellar lamella large, thin immersed.

Type locality: Occoquan, Virginia.

Geographic distribution: According to Pilsbry (1948:881) "Eastern United States and Canada, Maine, Ontario and Manitoba, south Miami, Florida, and Veracruz, Mexico; Cuba and Jamica (probably introduced)" *G. contracta* occurs in Kansas as far west as Reno and Kingman counties (Franzen and Leonard, 1947:331).

Ecology: Since *G. contracta* is primarily an eastern species it is not abundant in Kansas, although it is fairly well distributed throughout the eastern division of the state. It is found principally "on shaded slopes along the watercourses, under dead wood, leaf mold and grass" (Franzen and Leonard, 1947:331).

Archer (1939:22) reported this species in Michigan, "in deep grass in marshes; in ferns in meadows; under logs in birch-maple swamp woods; . . . This snail is nowhere common." On the Reservation *G. contracta* was found in six of the eight terrestrial habitats, but was not abundant at any of these. It was most numerous on the south facing slope (SG) where it occurred under forest litter in the more poorly drained areas on the hillside. Its occurrence on the north facing slope (SE) was limited to the poorly drained region near the bottom of the hillside where it was found under a heavy layer of humus composed, chiefly, of the leaves of the black oak and elm. Other equally favorable habitats were: in loose soil and under leaves on the banks of the small stream (SC); in and around decaying logs (SD); in loose soil around roots of small trees and shrubs at Station F; in loose soil among the roots of tall grass and weeds (SH).

Gastrocopta holzingeri (Sterki)

Plate CI, fig. 13

Pupa holzingeri Sterki, 1889, Nautilus, 3:37, 96, 119.
Gastrocopta holzingeri, Pilsbry, 1948, Acad. Nat. Sci. Philadelphia Monographs No. 3, 2(2):883-884, fig. 474.

Recognition characters: Shell small, oval; height 1.6 mm. to 1.9 mm.; rimate; whorls 5; aperature broadly oval; 7 lamellae and folds; angulo-parietal lamellae incompletely fused to form a mirror image of the letter "y"; heavy palatal callus; columellar lamella high, elongate.

Type locality: Will County, Illinois.

Geographic distribution: "Ontario and western New York to Helena, Montana, south to Illinois, Kansas, and Albuquerque and Mesilla, New Mexico" (Pilsbry, 1948:883). This snail has been collected from scattered localities over most of Kansas (Franzen and Leonard, 1947:335).

Ecology: Gastrocopta holzingeri is a northern species and not one of the dominant species of the fauna of Kansas (Franzen and Leonard, 1947:335). It has succeeded in adapting itself to the hot, dry summer months and, strangely enough, is to be found in many of the far western counties of the state.

Although *G. holzingeri* was found at five stations on the Reservation, it was abundant at only two of them (table 1). In the more moist areas on the west facing slope (SF) this species was the most numerous of the molluscan assemblage. Here it was found under the decaying leaves of the yellow oak and other forest debris. The species was not so abundant on the south facing slope (SG), but it was still common. A few specimens were collected from the banks of the small stream, from under decaying logs, and from under small stones in a rocky gully.

Gastrocopta pentodon (Say)

Plate CI, fig. 12

Vertigo pentodon Say, 1821, J. Acad. Nat. Sci. Philadelphia, 2:375.
Gastrocopta pentodon, Pilsbry, 1948, Acad. Nat. Sci. Philadelphia Monographs No. 3, 2(2):886-889, fig. 477.

Recognition characters: Shell small, usually 1.5 mm. to 2.0 mm. in height; whorls 5; 5 to 7 lamellae and folds; denticles variable in size and shape; thick callus immediately below peristome; fused angulo-parietal typically straight, simple, but in many specimens fusion is incomplete.

Type locality: Pennsylvania.

Geographic distribution: "Eastern United States and Canada: Prince Edward and Magdalen Islands to Alberta, south to central Florida and Texas; New Mexico; west in Arizona to the Santa Cruz River. Eastern Mexico and Guatemala. This species is found over a greater area than any other North American Gastrocopta" (Pilsbry, 1948:888).

Ecology: There has been, in the past, some confusion as to whether Kansan specimens assigned to this species were correctly identified or whether they should properly be referred to *Gastrocopta tappaniana* (C. B. Adams) (Pilsbry, 1948:889). Two distinct "forms" have long been recognized in the local fauna; a broad ovoid type and a smaller, more elongate form. In recent years workers have been inclined to consider both "forms" as *G. tappaniana.* It has been the experience of those working with the local fauna that specimens of both "forms" are highly variable in size and shape, and in many localities specimens may be arranged in a graded series from the slender "pentodon" to the broad "tappaniana" type. Specimens from the University of Kansas museum collection that had been identified as *G. pentodon* and *G. tappaniana* were examined and the literature concerned with these species reviewed. It is our opinion, that the characters used to separate specimens of *G. pentodon* and *G. tappaniana* are inadequate for the retention of specific rank and by the law of priority the name *G. tappaniana* should be considered a synonym of *G. pentodon.*

On the Reservation, specimens of *G. pentodon* were collected from all the wooded slopes, occurring more abundantly on the drier west and south facing hillsides than on the north facing slopes. These specimens from the hillside were predominantly of the smaller, more elongate form. The broad ovoid type was found only as dead specimens in moist situations along the banks of the small stream. When more ecological information concerning this species is acquired these two "forms" may be accorded subspecific rank.

Gastrocopta procera (Gould)

Plate CI, fig. 15

Pupa procera Gould, 1840, Boston Jour. Nat. Hist., 3:401; 4:359.
Gastrocopta procera, Pilsbry, 1948, Acad. Nat. Sci. Philadelphia Monographs No. 3, 2(2): 907-908, fig. 492.

Recognition characters: Shell medium in size for genus; height 2 mm. to 3.2 mm.; cylindric; rimate; whorls 5 to 6½; aperature rounded; peristome thickened within; deep excavation at upper extremity of outer lip; 6 lamellae and folds; a bifid angulo-parietal;

lower palatal more deeply placed than upper palatal or basal fold; columellar lamella nearly one half length of a whorl.

Type locality: Baltimore, Maryland.

Geographic distribution: "Eastern United States, Maryland to South Carolina, west to Shawnee Co., Kansas and Payne Co., Oklahoma; south to Alabama and eastern Texas" (Pilsbry, 1948:907). *Gastrocopta procera* has a wide distribution in Kansas (Franzen and Leonard, 1947:343, fig. 8).

Ecology: As can be seen by its southern distribution, *G. procera* prefers higher temperatures than those which prevail in the northern states. Its success in Kansas is due to its ability to withstand periods of drouth along with the prevailing high temperatures of the summer months. While it favors timbered hillsides, it shuns extremely moist situations.

On the Reservation, *G. procera* is nowhere abundant, although it occurs at five of the eight terrestrial stations. It is most numerous at Station H where it occurs in the loose soil among the roots of tall grass and weeds. The species is rare at Stations C, F, and G, being found under decaying humus in all three situations. A single, small specimen was collected from under cow dung in the grazed meadow. This was the only occurrence of a snail in the grazed meadow any appreciable distance from the timbered slopes which border the pasture.

Vertigo ovata Say

Plate CI, fig. 14

Vertigo ovata Say, 1822, Jour. Acad. Nat. Sci. Philadelphia, 2:375; Pilsbry, 1948, Acad. Nat. Sci. Philadelphia Monographs No. 3, 2(2): 952-953, fig. 513.

Recognition characters: Shell small, approximately 2 mm. in height; ovate; rimate; whorls 5, convex, striate; body whorl greatly enlarged, ⅝ height of shell; aperature oval, biarcuate; denticles 6 to 9; parietal lamella high, elongate; angular lamella low, tubercular; denticles on a heavy callus.

Type locality: Philadelphia, Pennsylvania.

Geographic distribution: "Prince Edward I[sland] and Ungava Bay, Labrador, south to Florida Keys and Texas, west to Puget Sound and Oregon, southwest to Fruita, Utah, Tempe and Huachuca Mts., Arizona. Alaska on Kodiak and Tigalda Is. West Indies" (Pilsbry, 1948:953).

Ecology: Vertigo ovata is an inhabitant of moist situations, and is uncommon in Kansas, being unable to adapt itself to the periodic drouths which obtain in that state. The species is found among

vegetation in swampy areas and along the banks of streams and other bodies of water.

Only two weathered shells of *V. ovata* were found on the Reservation. These were in loose soil on the steep banks of the small stream. It is unlikely that the living snails can be demonstrated from this habitat for, at present, the banks of the stream represent drier situations than *V. ovata* will normally tolerate.

Pupoides albilabris (C. B. Adams)

Plate CI, fig. 22

Pupa albilabris C. B. Adams (Ward's letter), 1841, American Jour. Sci., 40:271.
Cyclostoma marginata Say, 1821, Jour. Acad. Nat. Sci. Philadelphia, 2:172.
Pupoides albilabris, Pilsbry, 1948, Acad. Nat. Sci. Philadelphia Monographs No. 3, 2(2):921-923, fig. 499.

Recognition characters: Shell elongate-conic; height variable, usually 4.5 mm. to 5.6 mm.; whorls 4½ to 6½; aperature oval with a sinulus at the upper extremity of the outer lip; peristome heavy, reflected; no lamellae or folds present.

Type locality: Ohio.

Geographic distribution: "Eastern North America from Ontario and Maine to the Gulf of Mexico, west to the Dakotas, Colorado, and western Arizona; in northern Mexico on islands in the Gulf of California, at Monterrey and Tampico. Cuba; Haiti; Porto Rico; Bermuda" (Pilsbry, 1948:923). "Its occurrence in Kansas is general" (Franzen and Leonard, 1947:371).

Ecology: This widely distributed snail is unusual in its ability to flourish in arid regions as well as in those of more than moderate annual rainfall. In Michigan, Archer (1939:23) reported that *Pupoides albilabris*, "apparently does not occur in woodland cover." In 1937 Archer wrote of *P. albilabris* in Ohio, "*Gastrocopta armifera* and *Pupoides marginatus* are rare or absent in woods, but abundant in fields, on railroad embankments, and also in rocky, open country."

In Kansas, *P. albilabris* is found in woodlands as well as in open country. Franzen and Leonard (1947:371) report the species as occurring "in woodlands, in deep grass, or even among the roots of short grass in unshaded areas."

On the Reservation, *P. albilabris* was collected from three stations (table 1). It was abundant in the steep, well-drained areas of the west-facing, wooded slope (SF). The species was common on limestone ledges at the summit of the north-facing slope and a few specimens were collected from the loose soil around the roots of tall grass and weeds (SH).

Succinea avara Say

Plate C, fig. 8

Succinea avara Say, 1824, in Appendix to Keating's Narrative Exped. Source St. Peter's River, etc., Major Long's Second Expedition, 2:260, pl. 15, fig. 6; Pilsbry, 1948, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(2):837-840, fig. 455a to k.

Recognition characters: Shell ovate, yellowish, translucent; height variable, usually a little less than one-half inch; whorls 3 to 4; spire only one fourth height of shell; aperature oval; lip thin, simple; surface sculptured with growth lines, irregularly spaced.

Type locality: Northwest Territory.

Geographic distribution: "Newfoundland; Ontario north to James and Hudson Bay; north to Lat. 62 degrees on the Makenzis River; British Columbia; south to Florida in the east and to Northern Mexico in the west" (Pilsbry, 1948:837). This species is widely distributed in Kansas.

Ecology: Franzen and Leonard (1943:425), in referring to the occurrence of *S. avara* (incorrectly identified as *S. grosvenori*) in Northeastern Kansas, report, "while it is widely distributed in a variety of habitats, it apparently thrives best on the grass and reeds near or above the water in roadside ditches and similar situations." Its distribution in Kansas reflects its ability to withstand dry periods.

On the Reservation, *S. avara* is restricted to the more moist habitats (table 1). It is probably more common than the collections would indicate, owing to the fact that, in life, the shell is often daubed with dirt, making it almost invisible to the collector. The species was most common under decaying vegetation on the banks of the small stream (SC) and among the moss-covered, limestone rocks near the summit of the north and west-facing hillsides. It was collected also from under decaying logs on the north-facing slope.

Succinea concordialis Gould

Plate C, fig. 3

Succinea concordialis Gould, 1848, Proc. Boston Soc. Nat. Hist., 3:38.
Succinea concordialis, Pilsbry, 1948, Acad. Nat. Sci. Philadelphia, Monographs no. 3, 2(2): 833, fig. 452.

Recognition characters: Shell elongate-oval, thin, horn-colored, glossy; spire shortly conic; height variable, usually 15 mm. to 19 mm.; whorls 3; body whorl greatly inflated, marked by fine growth lines; aperture oval, ⅞ height of shell; lip thin; usually light callus over columella.

Type locality: Lake Concordialis (an abandoned meander of the Mississippi River opposite Natchez, Mississippi), Concordia county, Louisiana.

Geographic distribution: Southern and southeastern United States. Kansas records are from widely scattered localities.

Ecology: Little or nothing has been written concerning the ecology of this species. It is one of the most hygrophilic species of the genus. Its usual habitat is upon plants growing in or near the water. Only rarely is it seen actually submerged. The Succineas are often termed "amphibious" because they usually prefer moist situations.

No living specimens of S. *concordialis* were collected from the Reservation, but like other snails from the pond (SB), the empty shells were found in abundance while the pond was dry during the fall and early winter months. The number and appearance of these shells indicated that the pond had recently supported a large population.

Vallonia parvula Sterki

Plate CI, figs. 18, 19

Vallonia parvula Sterki, 1893, Man. Conch., 8:254, pl. 32, figs. 23-26; Pilsbry, 1948, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(2):1027-1028, fig. 547.

Recognition characters: Shell depressed, less than 1 mm. in height; diameter 1.6 mm. to 2.0 mm.; spire slightly convex; large, round umbilicus; whorls 3 to 3½; peristome strongly reflected; last two whorls with prominent ribs.

Type locality: Joliet, Illinois.

Geographic distribution: Pilsbry (1948:1028) lists localities from Ontario, Ohio, Illinois, Iowa, South Dakota, Kansas, Oklahoma, and Texas. A more exact statement of the distribution of this species can not be given until the relationships between it and closely related kinds are better known.

Ecology: This highly successful snail is found throughout Kansas in a wide variety of habitats. Franzen and Leonard (1943:423) reported this species as occurring "under logs or stones, where there is considerable moisture, although it will survive arid periods." Alice Leonard (1943:240) in reporting on the Mollusca of western Kansas characterized this snail as successful in that arid country where large numbers were found even in ravines that had scant timber.

The occurrence of *V. parvula* on the Reservation reflects its ability to live under a variety of situations. It was recovered from seven of the eight terrestrial habitats and was common at all but one of these (table 1). Its association with *Gastrocopta armifera* and *Retinella indentata* is noted elsewhere. *Vallonia parvula* was exceptionally abundant at Station G where, in some areas, the dead and living specimens averaged nineteen per square foot. Here and on other wooded slopes it was found in loose soil under a thin layer of decaying vegetation. Although it was common in more moist situations (SC, SD, and SF) it never reached the abundance demonstrated at Stations F and G. The species was collected also from arid limestone ledges and under small stones on rocky slopes.

Strobilops labyrinthica (Say)

Plate CI, fig. 16

Helix labryinthica Say, 1817, J. Acad. Nat. Sci. Philadelphia, 1:124.
Strobilops labyrinthica, Pilsbry, 1948, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(2):854-856, fig. 463.

Recognition characters: Shell small, conic; 2.0 mm. to 2.6 mm. in diameter; height approximately 2 mm.; whorls 5 to 6; suture distinct; three elongate lamellae, two of which can be seen at the aperature on the parietal wall; shell heavily sculptured with oblique ridges.

Type locality: Philadelphia, Pennsylvania.

Geographic distribution: "Maine and Quebec west to Manitoba, Minnesota, Kansas, and Arkansas, south to Georgia and Alabama" (Pilsbry, 1948:854).

Ecology: Strobilops labyrinthica is definitely a woodland snail. Pilsbry (1948:854) states that, "Its usual stations are under loose bark of logs, in half-decayed wood, among dead leaves and in sod at bases of trees." Franzen and Leonard (1943:423) noted that it was confined to moist woodland habitats in northeastern Kansas.

On the Reservation, the optimum habitat seemed to be around moist logs that were in advanced stages of decay. The snail is probably much more numerous than the collection would indicate, as the dull-brown shell is often hard to discern against the background of a decaying log. This species is often associated with *Zonitoides arboreus* and *Retinella electrina*. *S. labyrinthica* was also found beneath forest litter in oak-elm and oak-hickory-walnut areas on the north-facing slope (SE). The occurrence of this species on the arid limestone ledges (table 1) is no doubt correlated with the presence of many old logs in the vicinity.

Helicodiscus parallelus (Say)

Plate CI, fig. 24, 25

Planorbis arallelus Say, 1821, J. Acad. Nat. Sci. Philadelphia, 2:164 (corrected to parallelus in the index, p. 467).
Helicodiscus parallelus, Pilsbry, 1948, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(2):625-628, fig. 339.

Recognition characters: Shell small, flattened, greenish white in color; about ¾ inch in diameter; spire slightly convex; umbilicus (if it can be termed such) broad, showing all the whorls; whorls 4, closely coiled; whorls show numerous, fine ridges parallel to the sutures; many specimens have 1 to 3 minute denticles on outer wall of aperture.

Type locality: Pilsbry (1948:627) has selected Council Bluffs, Iowa, as the type locality.

Geographic distribution: From the Atlantic coast as far west as Minnesota, South Dakota, Kansas, Oklahoma, and Arkansas. To Newfoundland, Quebec, and Ontario in the north, and south to Alabama and South Carolina (Pilsbry, 1948:626). This species occurs in Kansas as far west as Meade County.

Ecology: Although *Helicodiscus parallelus* is widely distributed in Kansas, it is not abundant except in local situations. It is primarily a woodland inhabitant. Pilsbry (1948: 627) lists its habitats as "Decaying wood in shady or humid places, also on damp leaves . . . leaf siftings and in drift debris." In eastern Kansas the species may occur in grassy fields, on sparsely timbered slopes, and on rocky ledges as well as in more moist places. In the more arid parts of the state, however, *H. parallelus* is limited to woodland cover, and usually occurs around decaying timber.

Helicodiscus parallelus was nowhere common on the Reservation. The optimum habitats seemed to be the limestone ledges (SJ) and forest debris in the oak-hickory-walnut area on the north-facing slope (SE). It also occurred under decaying vegetation at Station F and G and among grass roots at Station H.

Stenotrema monodon aliciae (Pilsbry)

Plate C, figs. 5, 6

Polygyra monodon aliciae Pilsbry, 1900, Proc. Acad. Nat. Sci. Philadelphia, p. 455.
Stenotrema monodon aliciae, Pilsbry, 1948, Acad. Nat. Sci., Philadelphia, Monographs No. 3, 1(2):679-681, fig. 421c.

Recognition characters: Shell subglobose, light brown; diameter variable, approximately 6.5 mm.; spire dome shaped; base distinctly convex; approximately 6 whorls, closely coiled; white lip

reflected outward, innermost portion almost covering deep, round umbilicus; single denticle on parietal wall, sinuous, lying only partly within peristome; surface of shell covered with minute "hairs".

Type locality: Near Lake Charles, Calcasieu Parish, Louisiana (Pilsbry, 1946:680).

Geographic distribution: West to Kansas, Oklahoma and Texas; south to Mississippi and Alabama; east to Virginia and Maryland; north to Illinois and Indiana (Pilsbry, 1948:680).

Ecology: S. *monodon aliciae* is a woodland snail, usually found in moist situations. At the present time it is limited to the eastern section of Kansas. Franzen and Leonard (1943:410) wrote of it in northeastern Kansas as "distinctly a woodland snail, . . . thrives best in leaves, or near old stumps or logs among trees." Although not a colonial species, the snails often are numerous at a favorable site, such as the underside of a decaying log.

On the Reservation S. *monodon aliciae* was found in three of the selected habitats (table 1). It was most abundant in and around decaying logs on protected slopes. The species was common under forest litter in oak-elm and oak-hickory-walnut associations. Numerous bleached shells were collected from arid limestone ledges near the top of the north facing slope, but no living snails were observed.

Bulimulus dealbatus (Say)

Plate C, fig. 10

Helix dealbata Say, 1831, Jour. Acad. Nat. Sci., Philadelphia, 2:159.
Bulimulus dealbatus, Pilsbry, 1946, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(1):7-9, fig. 4.

Recognition characters: Globose-conic; mottled with grayish markings; height variable, usually 17 mm. to 23 mm.; whorls 6; umbilicus distinct, deep; aperature oval, large, one half height of shell; specimens in any single colony exhibit a great degree of variation in size and shape.

Type locality: Alabama? (Pilsbry, 1946:9).

Geographic distribution: Pilsbry (1946:9) lists localities from Alabama, Tennessee, Kentucky, Illinois, Missouri, Kansas, Oklahoma, Arkansas, Louisana, and Texas. The species is distinctly southern in distribution; the northernmost occurrences are in Missouri and Kansas.

Ecology: Bulimulus dealbatus differs from other species in the local fauna in being limited to open, arid country. The snail is colonial; many are often found on a single weed or bush upon

which they aestivate. At other times they are difficult to find, as they hibernate by burrowing in the soil. In Kansas, *B. dealbatus* has a scattered distribution, the colonies usually occurring on summit areas, often on bluffs along rivers and streams.

On the Reservation a colony of *Bulimulus dealbatus* was discovered near the pond in a weed patch. This small area, while a part of Station I, had been fenced off from the grazed part of the meadow. The adult snails were first observed on the tall weeds on June 11 and the young on June 20. Both the adults and the young preferred to aestivate on the dead stalks of last year's crop of weeds. Only two individuals were found on green vegetation. A few dead shells were collected from limestone ledges at the summit of the north-facing hillside.

Deroceras laeve (Muller)

Plate C, fig. 7

Limax laevis Muller, 1774, Verm. Terr. et Fluv. Hist., 2:2.
Limax gracilis Rafinesque, 1820, Ann. of Nat., 1:10.
Deroceras gracile, Baker, 1939, Ill. Nat. Hist. Survey Manual 2, p. 129-130; Franzen and Leonard, 1943, Univ. Kansas Sci. Bull., vol. 29, pt. 2, p. 425, pl. 32, fig. 25.
Deroceras laeve, Pilsbry, 1948, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(2): 539-552, figs. 289-291.

Recognition characters: Small, gray or black; body oval, elongate, terminating in a short carina; length about one inch; peduncles of eye long, tentacles short; foot narrow, whitish; mucus watery, not especially adhesive.

This slug can be recognized by its small size and its lack of distinct markings.

Type locality: Denmark.

Geographic distribution: "North America generally, from Arctic to middle Florida and Central America, the southern limit not determined" (Pilsbry, 1948:540).

Ecology: This small slug is common in wooded areas throughout Kansas. It is found in marshes, in woods, and on rocky slopes. It is active only when the relative humidity is high; at other times it retreats under stones, logs, leaves or any object that might serve as protection from the drying effects of the sun and wind. Although it is common, its small size and drab coloration make it difficult to find.

Deroceras laeve was collected from all the wooded slopes on the Reservation. It seemed to be most abundant in the poorly drained north-facing slopes. Here it was found around decaying logs and other forest debris.

Hawaiia minuscula (Binney)

Plate CI, figs. 20, 21

Helix minuscula Binney, 1840, Boston Jour. Nat. Hist., 3:435.
Hawaiia minuscula, Pilsbry, 1948, Acad. Nat. Sci., Philadelphia, Monographs No. 3, 2(1):420-424, figs. 228, 229.

Recognition characters: Minute, depressed; less than 2.5 mm. in diameter; spire only slightly elevated; whorls 4; suture well impressed; umbilicus round, wide, showing all the whorls.

Type locality: Ohio? (Pilsbry, 1946:423).

Geographic distribution: "It is generally spread over every eastern and midwestern state, and in Florida as far south as Miami and Cape Sable, though not seen from the Keys. It becomes rather local in the Rocky Mountain States, and has not been seen from Washington, Oregon, Idaho, Nevada, and Utah" (Pilsbry, 1946: 421).

Ecology: Although this small snail prefers a woodland environment, it is able to survive under arid conditions. Its occurrence in western Kansas is reported by Alice Leonard (1943:238).

On the Reservation, *H. minuscula* is not one of the most numerous species. It was collected from four of the eight terrestrial stations. While it was not rare at any of these, it was abundant only along the banks of the small stream (SC). Here, it was in the loose moist soil under a light layer of decaying vegetation. Other habitats included: under leaves in an oak-elm area (SE); among grass roots (SH); and under decaying logs on the north facing slope.

Retinella electrina (Gould)

Plate CII, figs. 28, 29

Helix electrina Gould, 1841, Invert. Massachusetts, p. 183, fig. 111.
Retinella electrina, Baker, 1930, Journ. Acad. Nat. Sci. Philadelphia, 82:196-198; Pilsbry, 1946, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(1): 256-259, fig. 126.

Recognition characters: Depressed; spire slightly convex; yellowish; 4.5 mm. to 5 mm. in diameter; whorls 4; suture shallow; umbilicus round, deep; peristome thin.

Type locality: Borders of Fresh Pond, Cambridge, Mass.

Geographic distribution: Southern and eastern Canada; Rocky Mountain States; North Central and Northeastern states. Southern limits are Arizona, New Mexico, Kansas, Missouri, and Virginia (Pilsbry, 1946:257).

Ecology: Retinella electrina is distinctly a woodland snail, occurring in leaf mold, under bark, and under decaying logs. It is

frequently associated with *R. indentata, Zonitoides arboreus,* and *Strobilops labyrinthica.*

Retinella electrina was recorded from four stations on the Reservation. It was abundant only on the north-facing slope, where it was found under decaying vegetation in oak-elm and oak-hickory-walnut associations, around decaying logs and stumps, and in moss at the bases of trees. This species was collected also from the banks of the stream and a few examples were recorded from the south-facing, wooded slope. *R. electrina* occurs far less frequently on the Reservation than does *R. indentata.*

Retinella indentata (Say)

Plate CII, figs. 30, 31

Helix indentata Say, 1823, Journ. Acad. Nat. Sci. Philadelphia, 2:372.
Retinella indentata, Baker, 1930, Journ. Acad. Nat. Sci. Philadelphia, 82:209-210; Pilsbry, 1946, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(1): 288-290, fig. 146.

Recognition characters: Depressed; spire slightly convex, yellowish; usually 4.0 mm. to 5 mm. in diameter; whorls 4; suture shallow; umbilical region indented but only slightly perforate.

Type locality: "Say gave localities in northern Philadelphia ("Harrigate") and New Jersey" (Pilsbry, 1946:289).

Geographic distribution: Southern Ontario and Quebec; south to Tennessee and northern Alabama; west to Shawnee Co., Kansas (Pilsbry, 1946:289).

Ecology: Retinella indentata is a highly successful snail, having a wide distribution and being found in a variety of ecological situations. Archer (1936:19) reports this species from such varied habitats as "in marsh grass . . . under rotten logs . . . around and under rock in the grass of the open fields; and on till among ironwood trees of the open slopes."

In Kansas, *R. indentata* is usually found on timbered slopes under stones, logs, loose bark, and other forest debris. It is rare in open country, although it occurs on rocky slopes having only a sparse cover of trees and shrubs.

On the Reservation, *R. indentata* was collected at all but one of the terrestrial stations (table 1). The association of *R. indentata* with *Gastrocopta armifera* and *Vallonia parvula* and the abundance of the three species has been noted elsewhere. At Station G the dead and living specimens of *R. indentata* averaged six per square foot. The species was most abundant under decaying vegetation at Stations G and F. Both of these slopes are covered with small

trees and brush and both are subject to the drying effects of the sun and wind. In this connection, it should be noted that *R. indentata* prefers drier habitats than does *R. electrina* although they frequently occur together in moist situations. Other habitats of *R. indentata* included the under sides of stones in rocky gullies, arid limestone ledges, the roots of deep grass and decaying logs.

Zonitoides arboreus (Say)

Plate CII, figs. 26, 27

Helix arboreus Say, 1816, (Nicholson's 1st American Edit. British Encycl., vol. 2, pl. 4, fig. 4.
Zonitoides arboreus, Pilsbry, 1946, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(1):480-483, figs. 261, 262.

Recognition characters: Shell depressed; spire slightly convex; dark brownish-yellow in color; less than 5 mm. in diameter; whorls 4½ to 5, growth lines fine, irregular; suture well impressed; lip thin, simple; umbilicus round, deep.

Type locality: Unknown.

Geographic distribution: Reported from all states except Nevada; as far north as Great Slave Lake in the Northwest Territory; as far south as Central America and the West Indies (Pilsbry, 1946:481).

Ecology: Zonitoides arboreus is one of the most widespread species of land snails in North America. In certain areas in the eastern and southern states the snail is an agricultural pest. In 1925 the root-rot disease, which was threatening Louisiana sugar cane industry, was traced to this species of snail; the snails feeding on the roots of the sugar cane damages the surface and permits the entrance of microorganisms from the soil (Johnson, 1925:70).

Zonitoides arboreus is not so abundant in Kansas as it is in the more eastern states, although it may be common in timbered areas. Its favorite habitats are around decaying logs, under loose bark, and among decaying vegetation (Franzen and Leonard, 1943:413). It is frequently found in association with *R. indentata* and *R. electrina.*

On the Reservation *Z. arboreus* was common on the north facing slopes, where it was found under decaying logs and under leaf humus in an oak-elm association. It was rare on the banks of the small stream and on the west-facing, wooded slope. The scarcity of *Z. arboreus* probably can be attributed to the absence of decaying logs on many of the wooded slopes.

Euconulus chersinus cf. *polygratus* (Pilsbry)

Plate CI, fig. 17

Conulus chersinus polygyratus Pilsbry, 1899, Nautilus, 12:116.
Euconulus chersinus polygratus, Pilsbry, 1946, Acad. Nat. Sci. Philadelphia, Monographs No. 3, 2(1): 240-241, fig. 119f.

Recognition characters: Small, globose-conic; light amber; rimate; whorls 5½ to 6, tightly coiled; aperture lunate; lip thin, reflected near columella; no lamellae or folds.

Type locality: Grand Rapids, Michigan.

Geographic distribution: "Ontario and Maine west in the northern tier of states to Wisconsin and to Malachi, Ontario, and Yonker, Saskatchewan" (Pilsbry, 1946:240).

On the Reservation, the species is nowhere abundant and it is limited to the wooded hillsides (table 1) where it occurs under rotten logs, decaying leaves, and other debris. It was collected from the three wooded slopes and occurred most frequently under logs on the north facing slope.

Sphaerium sp?

Plate C, fig. 1

Recognition characters: Oval, transversely inequilateral, inflated; epidermis brownish yellow; nacre bluish white; beak inflated, not prominent; anterior margin rounded; posterior margin somewhat blunt; sculpture fine, irregular; left valve: posterior lateral long, thin; anterior lateral short, high mid-way along ridge; right valve: posterior lateral double, upper posterior lateral small; anterior lateral small; cardinal teeth vestigial; anterior adductor scar prominent, others indistinct.

Ecology: Members of this genus and of the genus *Pisidium* belong to a group of bivalves that are not dependent upon the presence of fish for the completion of their life cycle. Without this restriction these species are able to occupy habitats that are prohibitive to fish, such as the ephemeral ponds and streams that are to be found throughout the state of Kansas. In Kansas, *Sphaerium* is more commonly found in streams than in ponds while the reverse is true of *Pisidium*.

On the Reservation, a species of *Sphaerium* was found in abundance in the silted pond (SB) where shells only were recovered, as the collecting was carried out during a period when the pond was dry.

Pisidium cf. *compressum* Prime

Plate C, fig. 4

Pisidium compressum Prime, 1851, Proc. Boston Soc. Nat. Hist., 4:164; 1865, Smithsonian Misc. Publ., No. 145, p. 64, fig. 68; Baker, 1928, Wisconsin Geol. Nat. Hist. Survey, Bull. 70, pt. 2, pp. 370-372, pl. C, figs. 9-13.

Recognition characters: Triangular, subequilateral, highly inflated; beak elevated, prominent; anterior margin bluntly rounded; posterior margin drawn out toward ventral margin; sculpture coarse, irregular; cardinals small; laterals short, high.

Type locality: "Massachusetts, in Fresh Pond, near Cambridge" (Baker, 1928:370).

Geographic distribution: "Over the continent, more common in East than in the West . . ." (Baker, 1928:371).

Ecology: As noted in the above discussion of *Sphaerium* species of the genera *Pisidium* and *Sphaerium* do not include a parasitic stage in their life cycle. *Pisidium* is found throughout Kansas in small ponds and streams. Alice Leonard (1943:234) reported the common occurrence of both *P. compressum* and *P. fabale* in Meade and Clark counties, Kansas.

Only a few bleached shells of this species were recovered from gravel in the bed of the small stream (SA) and it is possible that these are fossil.

SUMMARY

Some generalizations which can be made concerning the molluscan fauna of the University of Kansas Natural History Reservation are as follows:

1. The aquatic Mollusca are limited to four species: *Physa hawni, Pisidium compressum, Sphaerium* sp.?, and *Helisoma trivolvis,* all of which can survive long periods of drouth.

2. Three species of terrestrial snails, *Succinea concordialis, Vertigo ovata,* and *Lymnaea parva,* are found only in unusually moist situations close to water.

3. Only one species, *Bulimulus dealbatus,* is found exclusively in open areas. All of the other species were found on at least one of the wooded slopes.

4. Three species, *Gastrocopta armifera, Retinella indentata,* and *Vallonia parvula,* constitute, over most of the Reservation, between 60 and 80 percent of the total molluscan population.

5. *Gastrocopta armifera* is the most widely distributed snail on the Reservation, occurring in every terrestrial habitat.

6. *Vallonia parvula* is the most numerous of the terrestrial species.

7. The moist, north-facing slopes harbor a greater variety of species than the drier, south-facing slopes, but these south-facing slopes have more than twice as many snails per unit area as do the north-facing slopes.

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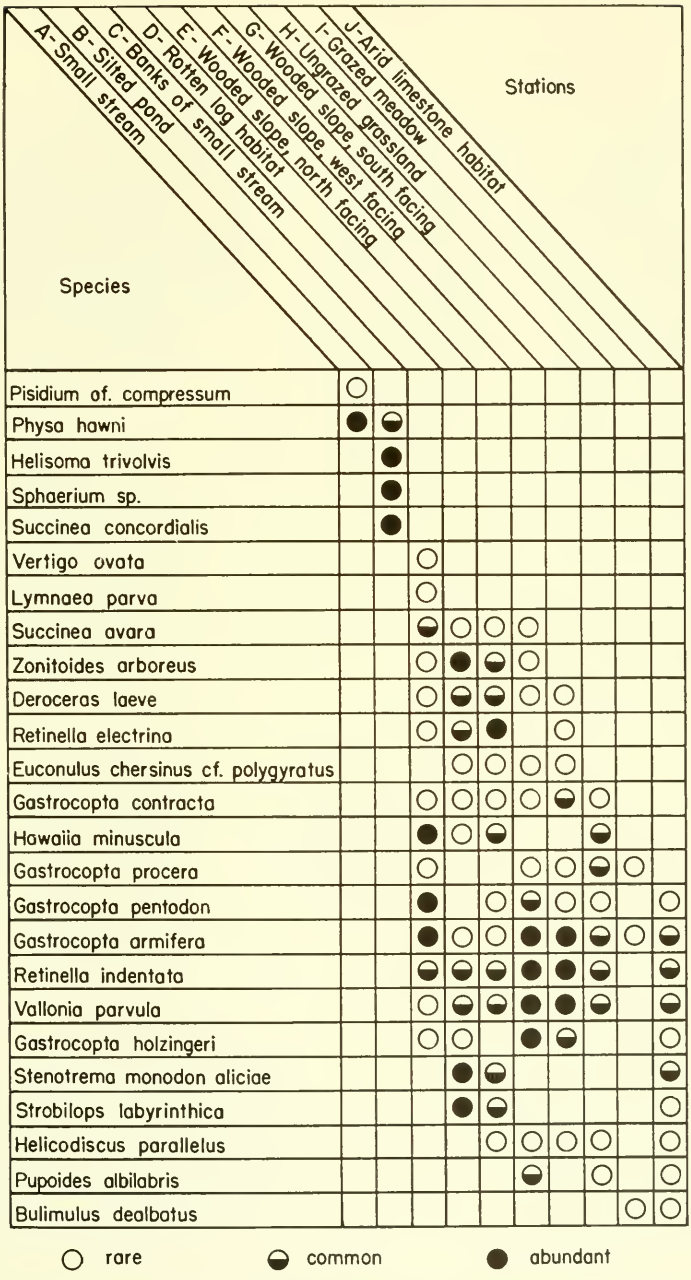


TABLE 1. Distribution on the University of Kansas Natural History Reservation of molluscan species according to habitat.

PLATE C

FIG. 1. *Sphaerium* sp.
FIG. 2. *Physa hawni.*
FIG. 3. *Succinea concordialis.*
FIG. 4. *Pisidium* cf. *compressum.*
FIGS. 5, 6. Basal and spiral views of *Stenotrema monodon aliciae.*
FIG. 7. *Deroceras laeve* (living animal).
FIG. 8. *Succinea avara.*
FIG. 8a. *Lymnaea parva.*
FIG. 9. *Helisoma trivolvis lentum.*
FIG. 10. *Bulimulus dealbatus.*
All figures enlarged $3\frac{1}{3}$ diameters.

PLATE C

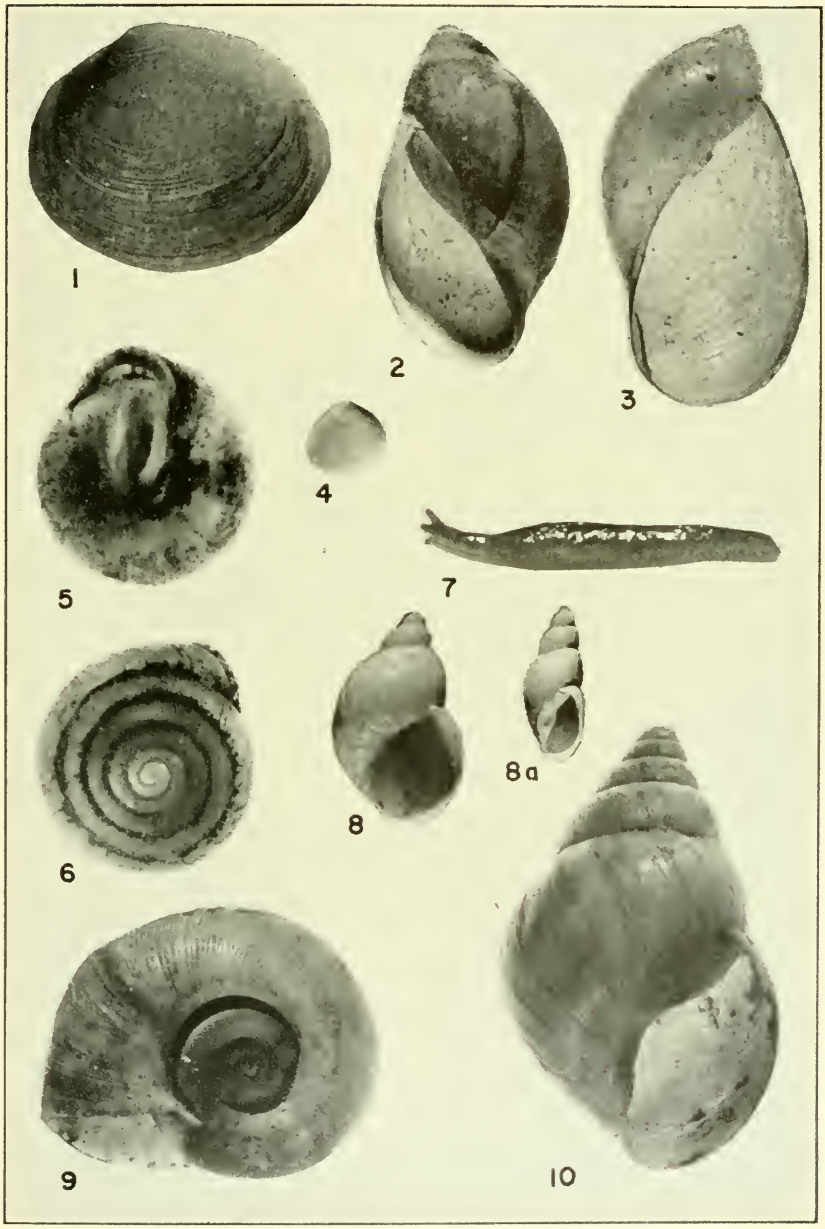


PLATE CI

FIG. 11. *Gastrocopta contracta.*
FIG. 12. *Gastracopta pentodon.*
FIG. 13. *Gastrocopta holzingeri.*
FIG. 14. *Vertigo ovata.*
FIG. 15. *Gastrocopta procera.*
FIG. 16. *Strobilops labyrinthica.*
FIG. 17. *Euconulus chersinus* cf. *polygyratus.*
FIGS. 18, 19. *Vallonia parvula,* spiral and basal views.
FIGS. 20, 21. *Hawaiia minuscula,* spiral and basal views.
FIG. 22. *Pupoides albilabris.*
FIG. 23. *Gastrocopta armifera.*
FIGS. 24, 25. *Helicodiscus parallelus,* spiral and basal views.
All figures enlarged 10 diameters.

PLATE CI

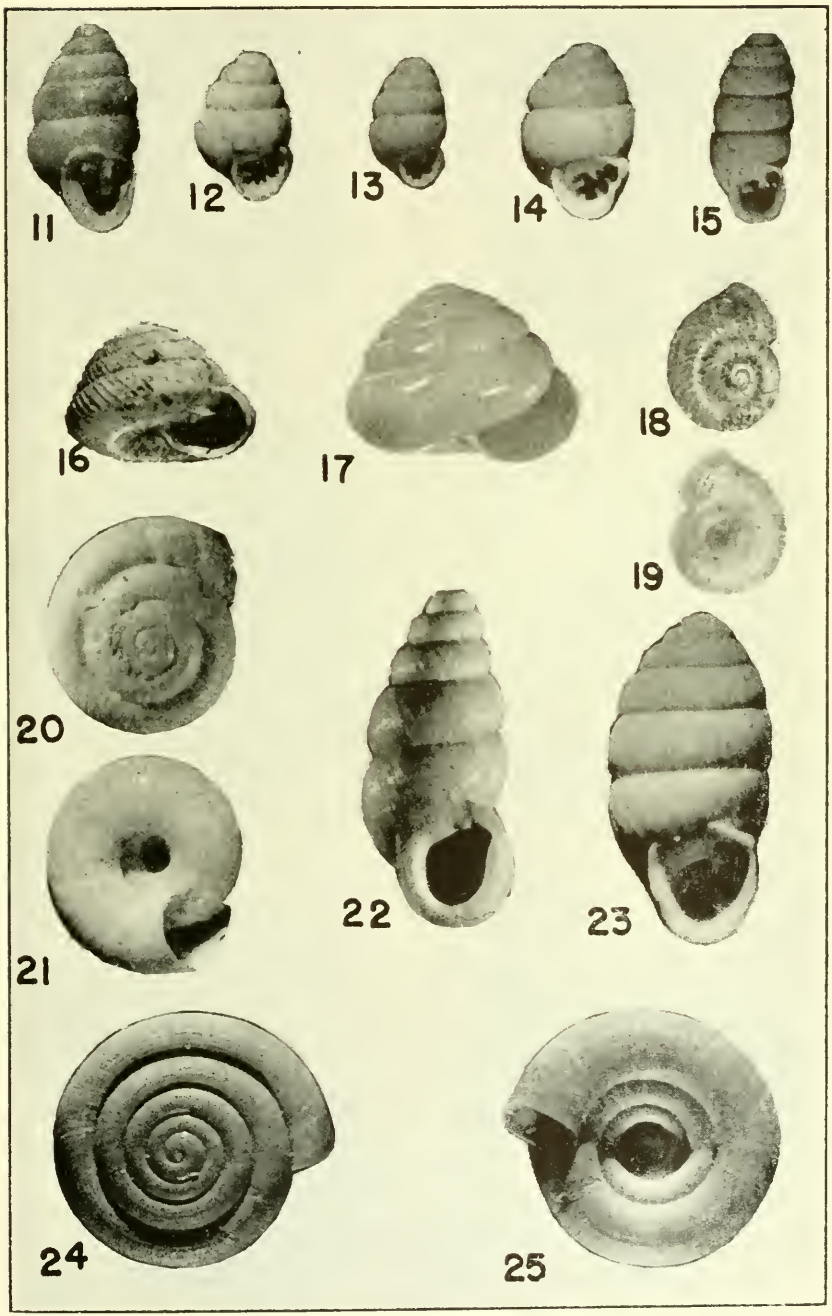
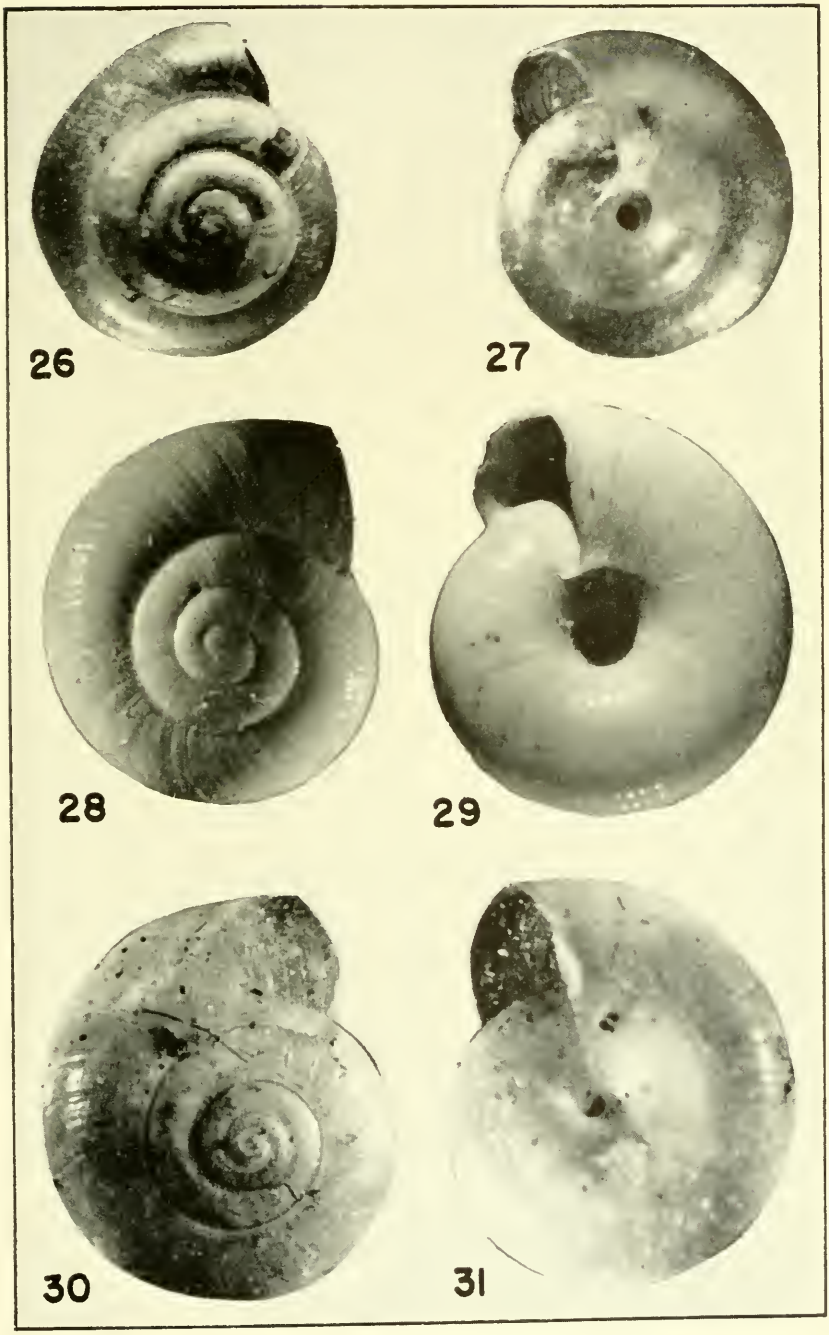


PLATE CII

FIGS. 26, 27. *Zonitoides arboreus,* spiral and basal views.
FIGS. 28, 29. *Retinella electrina,* spiral and basal views.
FIGS. 30, 31. *Retinella indentata,* spiral and basal views.
All figures enlarged 10 diameters.

PLATE CII



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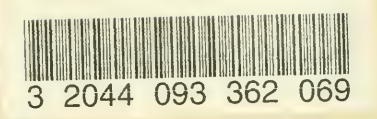
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